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IN MEMORIAM—A. PERRY PLUMMER (1911–1991): TEACHER, NATURALIST, RANGE SCIENTIST

E. Durant McArthur[1]

A. Perry Plummer died in the Gunnison Valley Hospital, Gunnison, Utah, on October 3, 1991, after several years of ill health. His passing deserves comment because he was a man who made a difference in natural resource management and research in the Intermountain area. He spent his professional career (1936–1979) with the Intermountain Research Station (INT, formerly the Intermountain Forest and Range Experiment Station) of the Forest Service, U.S. Department of Agriculture, at duty stations in Utah near Milford and in Ogden, Ephraim, and Provo.

TEACHER AND MENTOR

Perry was a caring, effective mentor and teacher. His assignment with the Forest Service was research and research administration, which he did well; but his professional love was teaching, especially small groups and individuals. His formal teaching was limited to a couple semesters at Brigham Young University (BYU) shortly after the 1975 establishment of INT's Shrub Sciences Laboratory on that campus. He established a wildland shrub biology class that remains a part of the BYU curriculum. In addition, he instructed numerous workshops at the Great Basin Experimental Range (Ephraim Canyon) and conducted many field tours at outplanting, common garden, range rehabilitation, and other research sites throughout Utah and the Intermountain area. Under these circumstances he was a master teacher whose points made lasting impressions on whoever was there—agency land manager, private landowner, public school teacher, Washington Office Forest Service research administrator, politician, junior colleague, or university professor.

Perry had a rare gift of integrating in his mind the potential vegetative states of degraded lands because he knew soil types, compatible plant associations, plant adaptations, planting equipment, and seedbed requirements. Because of this gift and his willingness to share it, he was often called on to consult those responsible for rehabilitating degraded lands. Typically, he would visit potential rehabilitation sites and follow up by providing detailed written recommendations. He completed well over one hundred careful, thoughtful consultations for the good of the land, for those who manage it, and for its human and other occupants. He was a mentor to others who continue on in this tradition; I think especially of Steve Monsen of our laboratory and Richard Stevens of the Utah Division of Wildlife Resources (DWR) in Ephraim.

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I illustrate Perry's teaching style with a personal example. In May 1972 I had been working for INT for four months when Perry took me on a field trip to the Brown's Park area of northeastern Utah to evaluate the results of some earlier work (he took or sent me on monthly field trips those first two or three years). At one stop I saw a patch of green in the distance at a spring. I suspected monkey flowers (*Mimulus* sp.—the subject of my Ph.D. degree research a few years earlier) would be growing there. I hustled over and confirmed my suspicion. Perry ambled up and said, "It's nice to appreciate these monkey flowers the way you do, but look back toward the truck. What else do you see? There are lots of other plant species and plant communities between here and there. You can learn a lot by looking at the whole plant community." He laughed in his characteristic way, and we discussed the various plant species present and their habitat requirements. A lasting lesson to me, it is similar to other Perry teaching moments shared by my colleagues.

BACKGROUND, EDUCATION, WORK ETHIC, AND HONORS

Arthur Perry Plummer (Fig. 1) was born on a farm in Daniel, Wasatch County, Utah, on April 10, 1911. His mother died when he was young; he and his siblings had a resourceful, independent upbringing with their widower father. He was educated in the Wasatch County public schools, at East High School in Salt Lake City, and at the University of Utah. Perry received a B.S. degree (1935) in botany from the U, began his INT career (1936), married Blanche Swindle of Monroe (1938), and completed his M.S. degree also in botany at the U (1939) in a busy four years. He enjoyed his university days and called on that background and experience throughout his career. Notable among his professors were Kim Newby, Walter Cottam, Ralph Chamberlin, Fayette Stephens, and Angus Woodbury. He and "Doc" Cottam continued a productive interchange of ideas and shared field trips into the mid 1970s.

Perry was a doer. He performed and worked hard. He didn't just ask his subordinates to get something done—he did it with them. As a new Ph.D., I didn't expect to be on the business end of a hoe for several hours a day, but then I didn't expect my boss to be in that situation either. He would show up anywhere a work crew was, ready to help with vigor and energy, and he expected anyone working to do the same. It wasn't uncommon for Perry to show up at these sites at 11:30 a.m. or 4:30 p.m., seemingly unaware of the impending lunch hour or quitting time.

Perry's record of accomplishment was noted by several organizations. In 1965 INT recognized him with a certificate of merit and a substantial cash award for outstanding performance in wildlife habitat research and application of that research. Also in 1965 the Utah Wildlife Federation honored him as Conservationist of the Year. In 1973 the Utah Chapter of the Soil Conservation Society of America gave him their Chapter Recognition Award. He received a USDA Superior Service Award in 1969 for implementing and making successful the cooperative work between INT and DWR. Perry, a 1949 charter member of the Society for Range Management (SRM), was president of the Utah Section and received SRM's Outstanding Achievement Award (1974), the premier Frederic G. Renner Award (1976), and the Fellow Award (1977). He was president of the Utah Chapter of the Soil Conservation Society during the early 1970s.

SCIENTIFIC CONTRIBUTIONS

In this section I comment not only on Perry's direct contributions but also on work that he stimulated and inspired. Perry's contributions were not limited to those he personally made; but, like those of many great teachers, his achievements have been enhanced and expanded by those who came after and built upon the foundation he laid.

Considering Perry's later contributions to shrub biology, it is of interest that his first publication was on developing a technique for preparation of microscopic sections of stems and roots of shrubs (Newby and Plummer 1936). His master's degree thesis (1939), published in 1943, dealt with germination and seedling development of range grasses. He continued his interest in seed germination, quality, storage, and processing, and in seedling development, on a wide range of plants throughout his career, and his successors have continued this work (Rudolf et al. 1974, Stein et al. 1974, Plummer

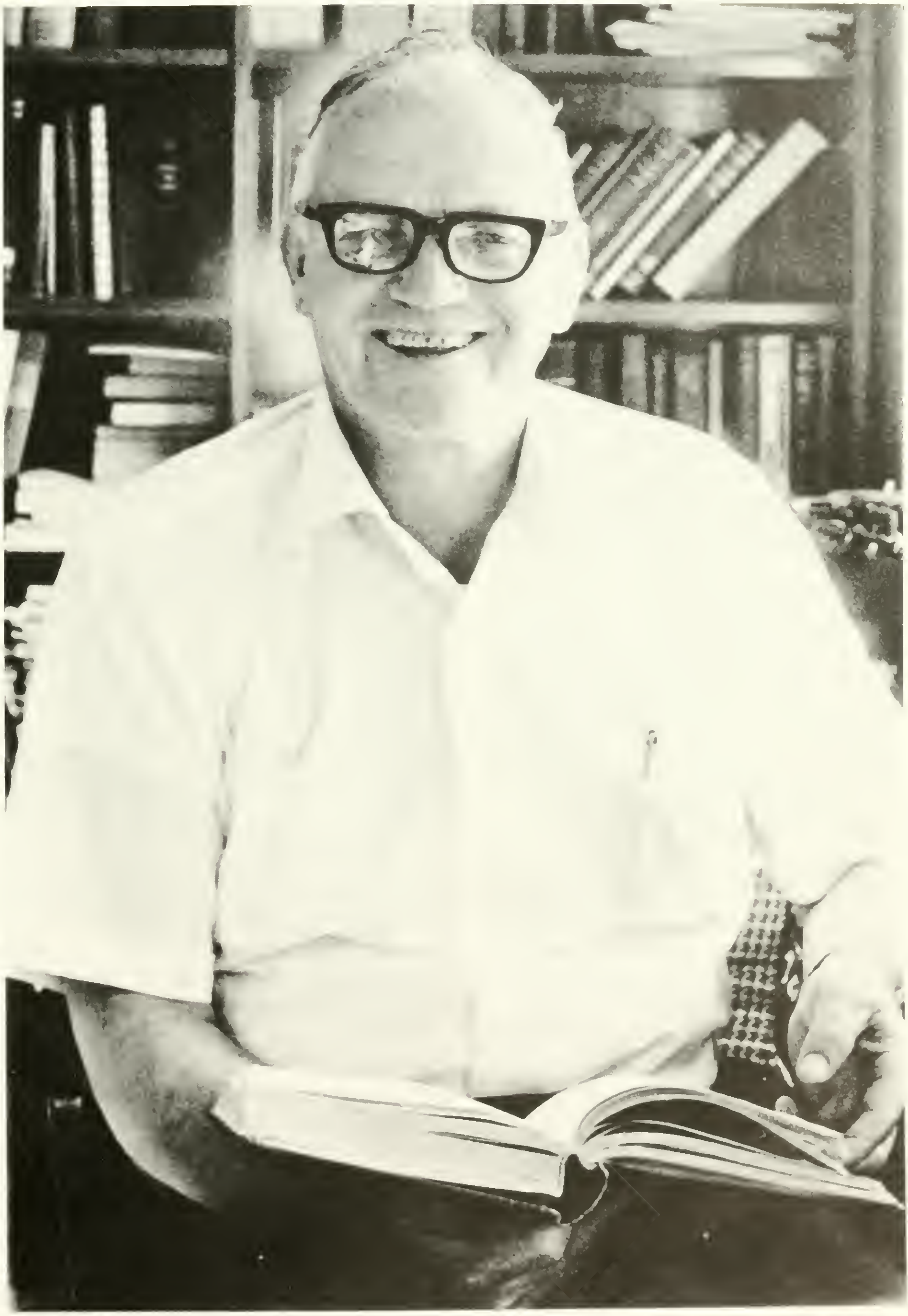

Fig. 1. A. Perry Plummer in his office about 1975.

and Jorgensen 1978, Stevens et al. 1981, Meyer et al. 1989, Stevens and Meyer 1990, Meyer and Monsen 1991).

Perry's greatest contributions involved development of procedures for revegetating degraded lands, including plant materials and operational equipment information and answers to how, when, why, and where. He was primary author of three "how to" publications that have been broadly accepted and applied (Plummer et al. 1955, 1968, Plummer 1977). The 1968 publication, Restoring Big Game Range in Utah, became a classic; it has been used extensively in the classroom and in the field and is now out of print after several press runs. It is serving as the foundation of a new compendium for western wildland rehabilitation techniques (Monsen and Stevens, in press).

Other publications of note for general and specific revegetation applications include Plummer et al. (1943), Stewart and Plummer (1947), Plummer and Fenley (1950), Plummer (1959, 1970), Plummer and Stapley (1960), Stevens et al. (1974), Harner and Harper (1976), Giunta et al. (1978a), McArthur et al. (1978b), Monsen and Plummer (1978), Stevens et al. (1981), Monsen and Shaw (1983), Monsen and McArthur (1985), Davis (1987), and Blauer et al. (in press).

His early revegetation work led to a cooperative research and application venture between INT and the Utah Division of Wildlife Resouces (known then as the Utah Department of Fish and Game) under Perry's direction. This effort was stimulated by big game winter range problems brought on by the partial urbanization of those ranges, large deer populations, and the heavy snowfalls of the late 1940s and early 1950s. The program began in 1954 at the behest of the directors of INT and DWR. It is the most extensive and longest running such arrangement in the country. He and his colleagues from DWR produced 11 substantive reports between 1956 and 1971 detailing their findings and recommendations in revegetation science (Plummer et al. 1956–1971). These reports, published by DWR, were sought out and used widely by land management professionals.

Perry had a particular interest in and impact on plant materials development including exploration, collection, evaluation, adaptation, culture, genetic variation, hybridization, and breeding systems. In this area he read carefully and followed the works of Luther Burbank (wide and unusual hybridizations, see Kraft and Kraft 1973), N. I. Vavilov and E. V. Wulff (origins and development of related plant groups, Wulff 1943, Vavilov 1951), Jens Clausen, David Keck, and William Hiesey (accessional or populational comparisons in common gardens and reciprocal transplantations, Clausen et al. 1940), and G. L. Stebbins (natural hybridization and intraspecific variation, Stebbins 1950, 1959). He was particularly interested in applying these concepts to western shrub species, which had received little prior attention despite their obvious ecological importance.

He spelled out his dream of a regional common garden testing scheme (LeGrande, Oregon; Boise, Idaho; Ephraim, Utah; and Reno, Nevada) in a 1972 document (Plummer 1972a). Although this dream was not fully implemented because of funding problems, several useful and interesting studies resulted—e.g., Van Epps (1975), McArthur and Plummer (1978), McArthur et al. (1978c, 1979, 1981), Welch and McArthur (1979, 1981), Welch and Monsen (1981), McArthur and Welch (1982), Edgerton et al. (1983), Welch et al. (1983), Geist and Edgerton (1984), Hegerhorst et al. (1987).

His specific interests in hybridization, breeding systems, and genetic variation and selection have been addressed in a series of publications specific to certain shrub taxa (Plummer et al. 1966, Nord et al. 1969, Hanks et al. 1971, 1973, 1975, Plummer 1974b, Blauer et al. 1975, 1976, McArthur 1977, Stevens et al. 1977, Giunta et al. 1978b, McArthur et al. 1978a, 1978c, 1979, 1988, in press, Welch et al. 1981, 1987, 1991, McArthur and Freeman 1982, Davis 1983, Freeman et al. 1984, 1991, Davis and Welch 1985, Welch and McArthur 1986, Pendleton et al. 1988, Welch and Jacobsen 1988, Wagstaff and Welch 1991) and in more general terms (Drobnick and Plummer 1966, Plummer 1972b, 1974a, Monsen 1975, Monsen and Christensen 1975, Carlson and McArthur 1985, McArthur 1989).

He had a keen eye for recognizing unusual and/or superior plant populations occurring naturally and in test plantings and in enhancing those materials for improved productivity and esthetics of degraded and badly disturbed lands. Several of these collections have been given distinctive 'cultivar' or source identified names and released for commercial propagation and use by his associates since his retirement. These include 'Appar' Lewis flax (*Linum perenne*), 'Cedar' Palmer penstemon (*Penstemon palmeri*), 'Rincon' fourwing saltbush (*Atriplex canescens*), 'Hatch' winterfat (*Ceratoides lanata*), 'Hobble Creek' mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana*), 'Immigrant' forage kochia (*Kochia prostrata*), 'Lassen' antelope bitterbrush (*Purshia tridentata*), 'Ephraim' crested wheatgrass (*Agropyron cristatum*), and 'Paiute' orchardgrass (*Dactylis glomerata*)

(McArthur et al. 1984, Monsen and Stevens 1985, Stevens and Monsen 1985, 1988a, 1988b, Stevens et al. 1985, Shaw and Monsen 1986, Welch et al. 1986, McArthur 1988). Other species and populations were not released but have had their usefulness documented and have become available in the revegetation species repertoire.

Perry Plummer served for many years as the Forest Service technical representative to the Western Regional Plant Introduction Committee (W-6). His plant materials expertise was put to use as a member of 1976 and 1977 plant collection and exploration teams in the Soviet Union (Dewey and Plummer 1980) and in 1980 as an on-site consultant in a New Zealand range rehabilitation program. He also stimulated interest in shrub disease and microbial and entomological relationships (Tiernan 1978, Nelson and Krebill 1981, Moore et al. 1982, Nelson 1983, Nelson and Tiernan 1983, Nelson and Schuttler 1984, Haws et al. 1988, Nelson and Lopez 1989).

Aspects of Perry's love of plants can be highlighted by two that were named after him: (1) 'Appar' Lewis flax was the first of several plant releases effected by INT, DWR, USDA Soil Conservation Service, and several state agricultural experiment stations (the "App" in Appar is for his initials); and (2) Grayia brandegei ssp. *plummeri* is a wide-leaved tetraploid variety of spineless hopsage that Howard Stutz named in honor of its discoverer (Stutz et al. 1987). These two plants illustrate the poles of Perry's work: one is a showy revegetation and horticultural cultivar; the other a restricted edaphic endemic, new to science.

Perry helped develop and refine equipment and techniques including anchor chaining, seed dribblers, scalpers, seed collection and processing, rangeland drills, and transplantation and interseeding equipment (Plummer et al. 1956–1971, 1968).

LEGACY

Many of Perry's 80+ publications are listed in the Literature Cited section. Aside from these, I see the following components of his legacy: (1) with Blanche, a fine family of seven children, (2) an expanded scientific foundation that he and his disciples have laid for wildland reclamation (see recent examples documented in the Literature Cited section) and for the incipient discipline of shrub science, (3) hundreds of thousands of acres of successfully rehabilitated wildlands that retain sufficient plant diversity to support a rich native fauna, and (4) a native wildland plant industry (several seed companies in Sanpete County alone owe their existence, at least in part, to Perry and his team for background information, collecting and processing techniques, and development of a market for products). I will address only item 2.

Perry began his career with the seeding, evaluation, and development of range grasses (Plummer 1944, 1946, Plummer and Stewart 1944, Plummer and Frischknecht 1952, Frischknecht and Plummer 1955). He was simultaneously involved in range management research (Roth and Plummer 1942, Plummer et al. 1943, Bleak and Plummer 1954) and sagebrush control work (Pechanec et al. 1944, 1954, 1965). Later, he managed the Great Basin Experimental Range in Ephraim Canyon (Keck 1972).

When his assignment changed to restoration of wildlife habitat in 1954, he quickly became converted to the value of shrubs on wildlands. Perry liked to recount his subsequent attempts to convert others to the value of shrubs, even the heretofore "weed" sagebrush, by recalling an anecdote. In the late 1950s he was with a crew on a vegetative rehabilitation project above a central Utah town. The local Forest Service district ranger came by to see what they were doing. Perry pointed out the various seeds in the seed mix—crested wheatgrass, orchard grass, alfalfa, fourwing saltbush, Lewis flax, small burnett, etc. The ranger wanted to know what one particular small black seed was. When Perry answered that it was sagebrush, the ranger took him to task for planting a weed. Perry acknowledged that he, himself, had spent much of his career trying to rid western lands of that plant but pointed out that it was needed for wildlife food and habitat. They were on a bench above a valley. Below them was recently cleared land that had been choked with a thick stand of sagebrush. Perry pointed out that there were good reasons to do both: thin sagebrush stands and plant sagebrush.

Perry had the vision to understand the usefulness of all plants within a community. He sought to include the use of less common but important taxa, including buckwheat, globemallow, and smooth aster. He understood that plants serve many important functions in addition to forage. He strongly supported management and restoration efforts needed to improve disturbed sites. His standing, knowledge, and ability to work with different people were extremely helpful to federal and state land management agencies as they attempted to balance livestock grazing pressure with carrying capacity of rangelands.

He was particularly interested in preservation and study of natural plant communities. He worked to maintain the exclosure facilities of the Great Basin Experimental Range and provided numerous plant vouchers for herbaria.

His work with shrub management and values was important in garnering support for construction of the Shrub Sciences Laboratory. V. L. Harper, retired Deputy Chief for Research, Forest Service, sent me a letter in 1985:

> I was doing a Research Inspection of the Intermountain Station (about 1960) . . . One of the centers Director Joe Pechanec and I visited was the work on shrub research. After listening to the Project Leader's (Perry's) presentation and viewing some of the field experiments, I turned to Joe and said "maybe we ought to amend the Ten-year Research Program to include a new laboratory at Provo . . . featuring shrub research including genetics, etc." Joe grinned broadly and said "I hoped you would see this need." He then produced a memo outlining the justification for such a laboratory to be located on the grounds of Brigham Young University. He further remarked, "I have outlined a speech which I can now cut short, giving a big pitch for the lab."

The laboratory was completed in 1975 (Stutz 1975). Perry and his colleagues saw great opportunities and benefits in wildland shrub research (Van Epps et al. 1971, McKell et al. 1972). Some of their vision has been realized (McKell 1989), one piece of evidence being a viable Shrub Research Consortium (Tiedeman 1984) headquartered at the Shrub Sciences Laboratory and involved with vital ongoing activities (McArthur 1990).

I was fortunate to visit Perry about two weeks before he died. He was at home between hospital stays. It was pleasant to update him on lab activities. He talked about his friends and colleagues who had gone on before and expressed the view that his time was near. Later, as I drove home, I reflected through misty eyes the good fortune I had of knowing and being mentored by the man. Many share this view.

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SECONDARY PRODUCTION ESTIMATES OF BENTHIC INSECTS IN THREE COLD DESERT STREAMS

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ABSTRACT.—We studied aquatic insect production in three cold desert streams in southeastern Washington. The Size-Frequency (SF) and P/B methods were used to assess production, which is expressed by taxon, functional group, and trophic level.

Dipterans (midges and black flies) were the most productive taxa, accounting for 40–70% of the total insect production. Production by collectors and detritivores was the greatest of all functional groups and trophic levels, respectively, in all study streams.

Insects with rapid development times and multiple cohorts are very important in cold desert streams; they were major contributors to the total insect production. Total insect production rates in our study streams (14–23 g $DW \cdot m^{-2} \cdot yr^{-1}$) were greater than those found in Deep Creek, Idaho (1.2 g $DW \cdot m^{-2} \cdot yr^{-1}$), the only other cold desert stream for which production data are available. Our values also were generally greater than published data for most cold/mesic (3–27 g $DW \cdot m^{-2} \cdot yr^{-1}$) and humid/mesic (3–25 g $DW \cdot m^{-2} \cdot yr^{-1}$) streams, but lower than in Sonoran Desert Streams (>120 g $DW \cdot m^{-2} \cdot yr^{-1}$) or New Zealand streams (~40 g $DW \cdot m^{-2} \cdot yr^{-1}$).

Our data support the contention of others that production, rather than density or biomass, is the most accurate and meaningful way to assess the role of these organisms in lotic ecosystems.

Key words: productivity, benthos, spring-streams, cold desert, functional groups, trophic levels, Diptera, Trichoptera, Coleoptera, Ephemeroptera, Odonata, Plecoptera.

Community-level production of insects has been assessed in relatively few stream types, and of all macroinvertebrates in even fewer. Particularly, little is known about secondary production in arid region streams. The only studies of secondary production in arid region streams that we are aware of are those of Minshall et al. (1973) in Deep Creek, Idaho, in the cold desert province, and Fisher and Gray (1983) and Jackson and Fisher (1986) in Sycamore Creek, Arizona, in the hot desert region.

Secondary production is the rate of animal tissue elaboration over time regardless of the fate (e.g., carnivory, emergence) of that production (Benke and Wallace 1980). Estimating secondary production in a stream provides one assessment of the role of animals in the ecosystem (Benke and Wallace 1980) as well as insight into ecosystem dynamics. Estimating only density and biomass, regardless of time, may not accurately describe the role of organisms in the stream. For instance, the role of gathering-collector invertebrates was underestimated by biomass analysis and overestimated by numerical analysis in a southeastern stream (Benke et al. 1984). Waters (1977) states that production is important to understanding ecosystem dynamics because it is the means by which energy is made available to higher trophic levels.

While most secondary production studies have focused on one or a few species in a stream (Benke and Wallace 1980, Waters and Hokenstrom 1980, O'Hop et al. 1984), more recent studies have estimated secondary production of the entire macrobenthic fauna (Krueger and Waters 1983, Benke et al. 1984, Smock et al. 1985, Huryn and Wallace 1987). Yet to be integrated into community-level analyses are the hyporheic fauna, protozoa, and other microinvertebrates. The community-level approach provides a more integrated insight into the ecology of stream ecosystems.

The purpose of this study was to measure the secondary production of insects in three streams located in the cold desert physiographic province of southeastern Washington. We emphasize

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TABLE 1. Physical and chemical characteristics of study reaches in Douglas Creek, Snively Springs, and Rattlesnake Springs, July 1985 to June 1986.

Stream	Average width (m)	Average depth (m)	Average discharge (m^3/s)	Dissolved O_2 (mg/L)
Douglas Creek	4.0	0.31	0.6	9.6–14
Snively Springs	1.3	0.10	0.04	8.6–12
Rattlesnake Springs	1.7	0.05	0.05	8.2–10

TABLE 2. Percent substratum types in study reaches of Douglas Creek, Snively Springs, and Rattlesnake Springs, July 1985 to June 1986.

	Substratum type				
Stream	Boulder (>256 mm)	Cobble (64–225 mm)	Pebble (16–64 mm)	Gravel (2–16 mm)	Sand/silt (<2 mm)
Douglas Creek	21	29	24	16	10
Snively Springs	7	20	25	11	37
Rattlesnake Springs	0	1	7	11	81

that the estimates published here are, in several cases, based on assumptions that we have explained (see Methods). Given the choices to which we could devote the available resources, we chose to produce an estimate of total insect production in these spring-streams rather than detailed data on a few taxa. We hope future studies will provide data on growth, CPIs, etc., for all taxa in these spring-streams which we can then use to refine the initial estimates presented here.

STUDY SITES

This shrub-steppe region is characterized by a climax community consisting of big sage (*Artemisia tridentata*) and bluebunch wheatgrass (*Agropyron spicatum*). Mean annual precipitation in the area is about 14 cm. The study streams were Douglas Creek (DC), Snively Springs (SS), and Rattlesnake Springs (RS) (Fig. 1). The average width, depth, discharge, and dissolved oxygen concentration for each study reach are shown in Table 1, and the substratum composition is given in Table 2. Figure 2 shows the daily and seasonal temperature ranges.

Douglas Creek

DC is a spring-fed stream located in Douglas County, Washington. It is the largest of the three streams studied, the stream itself draining an area of 530 km^2. Our study sites were located in the upper reaches where flow is permanent and not affected by irrigation withdrawal. Riparian vegetation is dominated by water birch (*Betula occidentalis*) and peachleaf willow (*Salix amygdaloides*).

Snively Springs

SS is a small spring-stream located on the U.S. Department of Energy's Hanford Site, Washington. It drains an area of approximately 40 km^2. The lower reaches of the spring-stream dry up during the summer, leaving about 3.6 km of perennial flow (Cushing 1988). Riparian vegetation is dominated by cattails (*Typha latifolia*) along the upper and lower reaches, and willow (*Salix* sp.) and wild rose (*Rosa* sp.) along the mid-reaches, where it flows through a canyon. Watercress (*Nasturtium officinale* = *Rorippa nasturtium-aquaticum*) grows extensively within the spring-stream.

Rattlesnake Springs

RS is a small spring-stream also located on the Hanford Site. It drains an area of 350 km^2 (Cushing et al. 1980). Portions of the lower reaches dry up during the summer, leaving about 2.5 km of perennial flow. Mean annual total alkalinity (as $CaCO_3$) is 127 ppm, and the spring-stream is subject to periodic severe spates in winter (Cushing and Wolf 1982, Cushing and Gaines 1989). Riparian vegetation is dominated by peachleaf willow and cattails.

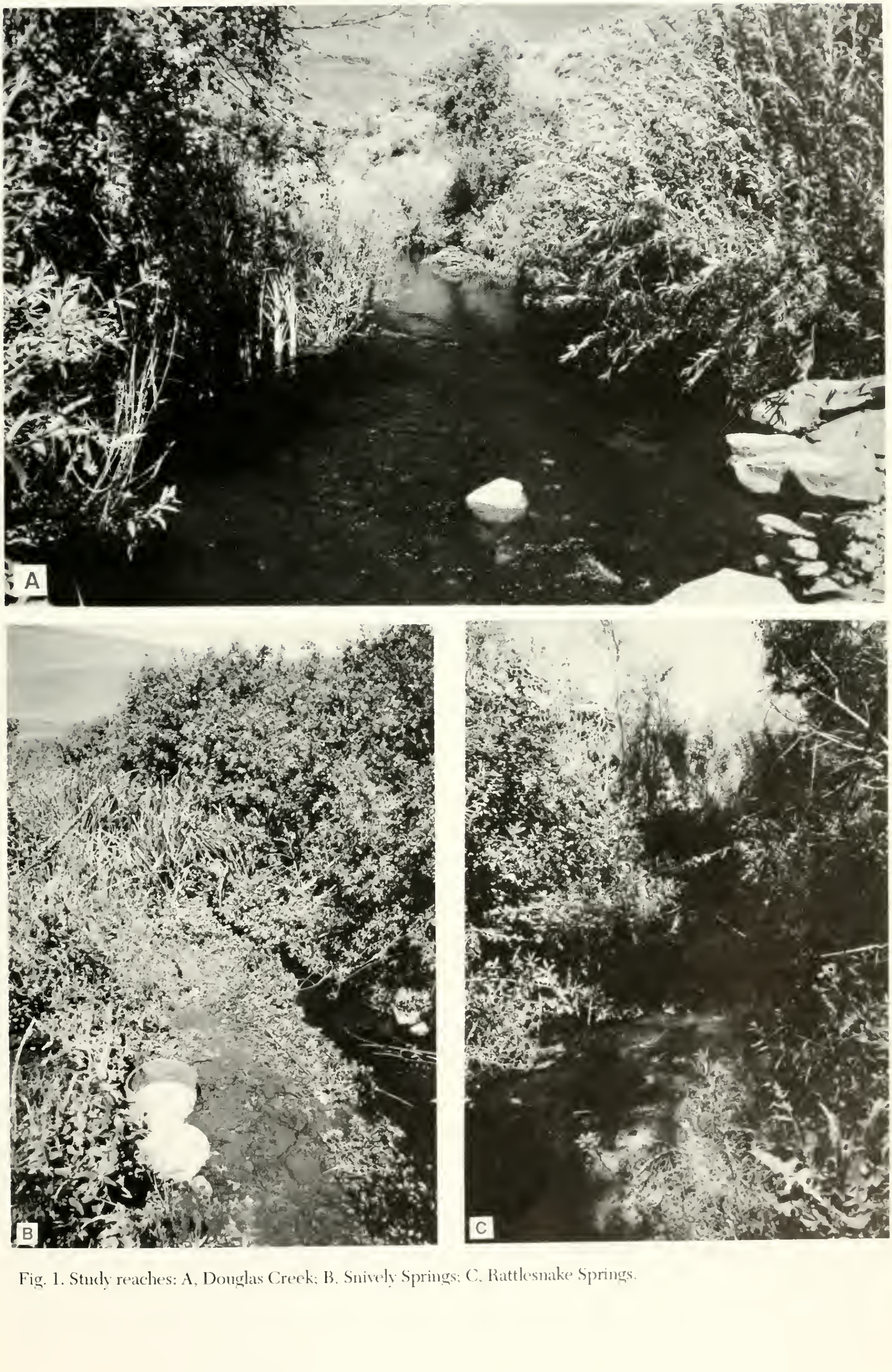

Fig. 1. Study reaches: A, Douglas Creek; B, Snively Springs; C, Rattlesnake Springs.

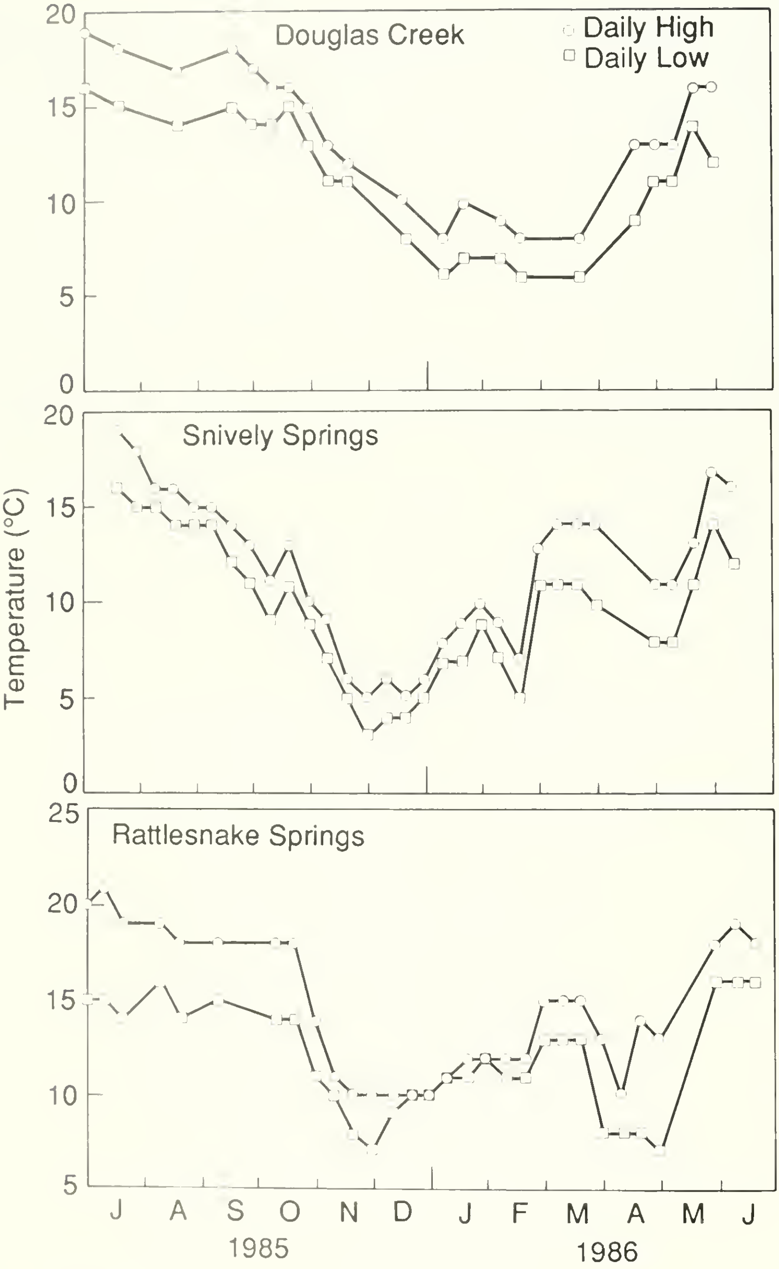

Fig. 2. [illegible] temperature regimes: Douglas Creek, Snively Springs, and Rattlesnake Springs, July 1985 to June 1986.

Watercress is presently the dominant in-stream autotroph, although periphyton primary production exceeded that of watercress in 1969–70 (Cushing and Wolf 1984).

METHODS

We sampled segments of each stream representing the various habitats that were present.

One study reach was sampled in SS and one in RS, and three reaches were sampled in the larger DC. Samples were taken to calculate an average standing stock for each stream to be used to calculate production estimates. The sampling scheme was not designed to allow intrastream comparisons of production estimates between different habitats, but rather to provide representative production estimates of the entire stream.

Samples were collected monthly from July 1985 through June 1986. We collected three samples during each visit. A Portable Invertebrate Box Sampler (PIBS) (0.1 m^2, mesh size 350 μm) was used in DC. A Surber sampler (0.09 m^2, mesh size 350 μm) was used in SS and RS because these spring-streams are too shallow for a PIBS. Samples were taken to a depth of 10 cm and preserved in 70% ethyl alcohol.

Insects were separated from organic debris by sugar flotation (Anderson 1959) and sorted by taxa. Insects were identified to the lowest taxonomic level possible and counted, and body length was measured to the nearest 1 mm using a microscope and ocular micrometer. The trophic status of each taxon was determined by examining gut contents (Gaines et al. 1989) or by reference to Merritt and Cummins (1984). Biomass was determined as dry weight (DW) for all size classes after drying at 60 C for 24 h and weighing to the nearest 0.1 mg.

The Size-Frequency (SF) method (Hynes and Coleman 1968, Hamilton 1969, Hynes 1980, Waters and Hokenstrom 1980) was used to estimate secondary production of the most common taxa. An average SF distribution was determined from monthly sample sets; these represented the survivorship curve of an "average cohort" (Hamilton 1969, Benke and Waide 1977); "zero" values were included when calculating densities. Production was estimated by calculating the loss between successive size classes and then multiplying the loss by the number of size classes using the equation given by Hamilton (1969). Production estimates were refined by multiplying by 365/CPI (Cohort Production Interval; Benke 1979).

We found that conducting growth studies for all taxa present within each of the streams was not practicable. To establish reasonable estimates of larval development times and CPIs, we followed the example of Benke et al. (1984), who used available life-history data and field data to estimate CPIs. We used three major sources of information to estimate CPIs for each taxon in our study streams. First, we surveyed the available life-history data gathered from literature reviews and extrapolated the results to apply to our situations. Second, we made field observations to determine presence/absence of taxa and collected size-frequency information for each taxon to estimate larval development times and CPIs. Lastly, we conducted in situ growth studies for *Baetis* sp., *Cheumatopsyche* sp., and *Simulium* sp. to allow further refinement of our CPI estimates. These growth studies involved placing insects within growth chambers in RS. Chambers were constructed with mesh netting on each end to allow water and food material to pass through. Measurements were taken and development times recorded to estimate CPIs. Using the combination of all these data sources, we feel confident that our CPI estimates are reasonable approximations.

Production/Biomass (P/B) ratios (Waters 1977) were used to estimate secondary production for less-abundant taxa. These P/B ratios were either taxon-specific values derived from the study streams or an assumed cohort P/B value of 5 (Waters 1977, Benke et al. 1984). These taxa were not present in sufficient numbers to provide an accurate SF distribution curve that is necessary to compute SF production estimates.

RESULTS

Production calculations for DC, SS, and RS are given in Tables 3, 4, and 5, respectively. The following text describes some of the assumptions we used in our calculations, data supporting these assumptions, and other information relevant to the production calculations. All production estimates, unless noted otherwise, are given in units of mg $DW \cdot m^{-2} \cdot yr^{-1}$.

Douglas Creek

EPHEMEROPTERA.—Mayflies typically exhibit widely varied larval development times (Clifford 1982). Clifford (1982) examined life-cycle data of 85 species of Heptageniidae and found that >90% had at least one univoltine cycle. Field data for *Baetis* sp. in DC provided little clarification of the CPI. Based upon field data of *Baetis* sp. from RS and SS, and a growth study in RS, we estimated a CPI of 60 d. Similar temperature regimes in DC and RS support this

TABLE 3. Annual production of insects in Douglas Creek, July 1985 to June 1986.

	365/CPI[a]	Calculation method	N/m²	SE	CV	B (mg DW/m²)	SE	CV	Annual production (mg DW/m²)	Annual P/B
Ephemeroptera										
Baetis sp. (gc, D)[b]	6°	SF[c]	2416	0.41	92.4	263.7	0.41	91.9	8320	31.5
Paraleptophlebia sp. (gc, D)	1	SF	225	0.35	78.5	48.1	0.38	85.4	249	5.2
Leucrocuta sp. (g, H)	1⁺	SF	160	0.47	104.0	51.4	0.51	104.0	238	4.6
Tricorythodes sp. (gc, D)	9	PBd	6	0.80	159.2	1.7	0.67	151.0	77	45.0e
TOTAL			2807			364.9			884	
Odonata										
Argia tibialis (p, C)	1⁺	PB	30	0.46	103.9	8.9	0.49	110.3	44	5.0[e]
Plecoptera										
Isoperla sp. (p, C)	1⁻	SF	77	0.58	129.4	42.8	0.58	113.9	183	4.3
Trichoptera										
Hydropsyche sp. (fc, D)	1⁺	SF	445	0.57	127.1	413.5	0.65	145.8	1700	4.1
Cheumatopsyche sp. (fc, D)	2+,°	SF	156	0.53	118.3	84.1	0.60	135.0	818	9.7
Leucotrichia pictipes (g, H)	1+,°	SF	95	0.63	139.7	7.7	0.68	153.2	32	4.2
TOTAL			696			505.3			2550	
Coleoptera										
Optioservus sp. (g, H)	1+	SF	4322	0.37	83.5	606.7	0.36	80.0	2160	3.6
Diptera										
Chironomus sp. (gc, D)	15°	PB	753	0.71	152.3	60.7	0.69	153.8	4920	81.1f
Simulium sp. (fc, D)	12°	PB	41	0.75	168.6	31.2	0.72	136.1	1680	54.0[f]
Parametriocnemus sp. (gc, D)	15°	SF	196	0.44	98.0	10.4	0.46	101.9	875	84.1
Chaetocladius sp. (gc, D)	15°	SF	115	0.57	127.8	3.5	0.66	129.4	426	121.7
Heleniella sp. (gc, D)	15°	SF	141	0.52	116.4	4.5	0.54	116.5	423	94.0
Tipulidae (s, D)	1°	PB	37	0.37	82.5	82.1	0.48	103.1	411	5.0[e]
Phaenospectra sp. (g, H)	9°	PB	60	0.07	15.5	4.9	0.07	15.0	221	45.0[e]
Polypedilum sp. (s, H)	18°	SF	33	0.69	154.5	2.2	0.78	129.1	161	73.1
Tabanidae (p, C)	1°	PB	51	0.48	106.6	27.8	0.48	107.5	130	5.0[e]
Thienemanniimyia sp. (p, C)	15	PB	11	0.81	180.5	0.9	0.83	185.4	75	83.6[f]
Brillia flavifrons (s, D)	15°	PB	12	0.25	55.0	0.9	0.26	57.4	68	75.0[e]
Empididae (p, C)	15	PB	1	0.22	50.0	0.1	0.18	40.0	8	75.0[e]
TOTAL			1451			229.2			9358	
GRAND TOTAL			9383			1757.8			23219	

[a] Source of CPI used: ° = derived from growth studies, + = field data and SF distributions, o = literature; - = based upon CPI for similar cited insects (used when other sources were not available).

[b] s = shredder, gc = gathering-collector, fc = filtering-collector, g = grazer/scraper; p = predator, H = herbivore, D = detritivore; C = carnivore.

[c] SF = production calculated by the Size-Frequency method.

[d] PB = production calculated by an assumed P/B ratio.

[e] Assumed cohort P/B of 5.

[f] Assumed annual P/B is the same as derived by SF for this taxon in one of the other study streams.

estimate. *Paraleptophlebia* sp. is generally univoltine, having either summer or winter cycles (Clifford 1982). In DC, however, seasonal cycles could not be distinguished. *Paraleptophlebia* were present in DC throughout the study year, and we assumed a CPI of 1 yr. Because of low numbers of *Tricorythodes* sp., field data provided little indication of their CPI. McCullough et al. (1979) reported a 34-d larval development time for *T. minutus* grown in the field at 18 C; therefore, we estimated a CPI of 40 d for *Tricorythodes* sp. because of lower stream temperatures in DC.

ODONATA.—The damselfly *Argia tibialis* is univoltine.

PLECOPTERA.—A CPI estimate for *Isoperla* sp. could not be made from field data. Several studies (Mackay 1969, Harper 1973, Barton 1980) of *Isoperla* sp. showed seasonal variation in growth rate, but generally their development time was about 1 yr. Therefore, we assumed a CPI of 1 yr.

TRICHOPTERA.—*Leucotrichia pictipes* was univoltine, and as SF distributions and field data indicated, the larvae overwintered as late instars and emerged in spring. This observation is supported by studies on *L. pictipes* in Owl Creek, Montana (McAuliffe 1982).

COLEOPTERA.—An accurate CPI estimate for the riffle beetle *Optioservus* sp. was difficult to estimate because few data are available concerning their development times. We thus assumed a CPI of 1 yr.

TABLE 4. Annual production of insects from Snively Springs, July 1985 to June 1986.

	365/CPI[a]	Calculation method	N/m^2	SE	CV	B (mg DW/m^2)	SE	CV	Annual production (mg DW/m^2)	Annual P/B
Ephemeroptera										
Baetis sp. (gc, D)[b]	6$^{+,o}$	SF[c]	1388	0.62	101.7	185.4	0.55	96.3	7010	37.8
Paraleptophlebia sp. (gc, D)	1^{+}	SF	54	0.27	47.5	15.5	0.28	48.2	67	4.3
TOTAL			1442			200.9			7077	
Odonata										
Argia tibialis (p, C)	1^{+}	PB[d]	22	0.61	106.6	27.8	0.68	118.6	139	5.0[e]
Trichoptera										
Cheumatopsyche sp. (fc, D)	2$^{+,-}$	SF	433	0.41	83.0	200.9	0.51	86.9	1300	6.5
Diptera										
Simulium sp. (fc, D)	12$^{+,-}$	SF	276	0.70	121.3	34.3	0.82	142.6	1880	54.8
Chironomus sp. (gc, D)	15°	SF	412	0.54	93.2	17.1	0.58	99.8	1390	81.1
Tipulidae (s, D)	1^{o}	PB	25	0.60	103.8	219.2	0.50	87.4	1100	5.0e
Heleniella sp. (gc, D)	15^{-}	SF	381	0.40	69.2	9.2	0.37	64.7	550	60.3
Polypedilum sp. (s, H)	18^{-}	SF	123	0.56	96.2	3.2	0.52	89.1	220	68.6
Chaetocladius sp. (gc, D)	15^{-}	SF	92	0.63	108.3	2.7	0.69	120.2	210	77.8
Dixidae (gc, D)	15^{-}	PB	21	0.55	95.9	1.3	0.65	111.5	98	75.0[f]
Thienemannimyia sp. (p, C)	15^{-}	PB	18	0.42	72.3	1.1	0.33	57.3	92	83.6[f]
Tabanidae (p, C)	1^{o}	PB	52	0.47	81.5	10.5	0.50	86.4	53	5.0[e]
Empididae (p, C)	15	PB	4	0.15	26.6	0.6	0.12	32.1	45	75.0[e]
TOTAL			1404			299.2			5638	
GRAND TOTAL			3301			728.8			14,154	

[a] Source of CPI used (° = derived from growth studies; + = field data and SF distributions; o = literature; - = based upon CPI for similar cited insects (used when other sources were not available).

[b] s = shredder; gc = gathering-collector; fc = filtering-collector; g = grazer/scraper; H = herbivore; D = detritivore; C = carnivore.

[c] SF = production calculated by the Size-Frequency method.

[d] PB = production calculated by an assumed P/B ratio.

[e] Assumed cohort P/B of 5.

[f] Assumed annual P/B is the same as derived by SF for this taxon in one of the other study streams.

DIPTERA.—*Simulium* sp. were not present in sufficient numbers in DC to calculate an SF production estimate. The P/B ratio was calculated by averaging the P/B ratios obtained for *Simulium* sp. in SS and RS by the SF method. Accurate CPI estimates for Chironomidae could not be obtained from field observations or SF distribution. Therefore, we derived CPI estimates, as did Benke et al. (1984), and used growth data from Mackey (1977). Mackey (1977) reported larval development times of 21 d for *Chironomus* sp., 13 d for *Polypedilum convictum*, and 36 d for *Phaenospectra flavipes* at 15 C. CPIs were compensated for slightly lower average temperatures in DC (13 C) and environmental stress (e.g., food availability, competition, etc.). These P/B ratios seem high but are comparable to other data where short CPIs were used to estimate P/B ratios (Benke et al. 1984, Jackson and Fisher 1986). Tabanidae and Tipulidae were assumed to be univoltine with a development time of 1 yr (Krueger and Cook 1984). This is consistent with the estimate of a 1-yr development time for *Tabanus dorsifer* in Sycamore Creek, Arizona (Gray 1981). Empididae grew to a maximum size similar to many of the midges; therefore, a CPI of 25 d was used.

Snively Springs

EPHEMEROPTERA.—Gray (1981) reported a larval development time of 20 d for *Baetis quilleri* in Sycamore Creek, Arizona. Because of lower stream temperatures, however, *Baetis* sp. developed more slowly in all streams in this study. We assumed a CPI of 60 d. *Paraleptophlebia* sp. was present only during the summer; thus, we used only summer data to calculate production because annual P was essentially equal to summer P.

ODONATA.—*Argia tibialis* was not present in sufficient numbers to make an SF production estimate.

TRICHOPTERA.—Field data and SF data indicated a bivoltine life cycle and a CPI of 6 mo for *Cheumatopsyche* sp., the only caddisfly in SS.

DIPTERA.—Becker (1973) reported a larval development time of 13 d for *S. vittatum* grown in the laboratory at 17 C. A 30-d CPI was estimated considering lower stream temperatures

TABLE 5. Annual production of insects from Rattlesnake Springs, July 1985 to June 1986.

	365 CPI[a]	Calculation method	N/m²	SE	CV	B (mg DW/m²)	SE	CV	Annual production (mg DW/m2)	Annual P/B
Ephemeroptera										
Baetis sp. (gc, D)[b]	6°+	SF[c]	1336	0.61	107.2	47.3	0.58	104.0	2540	53.8
Tricorythodes sp. (gc, D)	9	PB[d]	1	0.05	8.3	0.3	0.07	12.2	14	45.0[e]
TOTAL			1337			47.6			2554	
Odonata										
Argia tibialis (p, C)	1+	PB	67	0.72	124.1	74.3	0.78	134.9	372	5.0[e]
Trichoptera										
Cheumatopsyche sp. (fc, D)	2°+	SF	140	0.69	118.9	48.6	0.78	134.5	486	10.0
Parapsyche sp. (fc, D)	1-	PB	10	0.24	41.7	26.8	0.25	43.4	134	5.0[e]
Limnephilus sp. (s, D)	1-	PB	52	0.45	76.9	22.0	0.38	66.3	115	5.0[e]
TOTAL			202			97.4			735	
Coleoptera										
Hydaticus sp. (p, C)	1	PB	4	0.50	87.4	1.2	0.35	60.1	6	5.0[e]
Hydrophilidae (p, C)	1	PB	1	0.27	47.6	0.3	0.25	43.1	2	5.0[e]
TOTAL			5						8	
Diptera										
Simulium sp. (fc, D)	12°+	SF	1777	0.73	125.8	212.3	0.73	127.5	11,180	52.6
Chironomus sp. (gc, D)	15°	SF	192	0.50	87.3	7.0	0.58	100.8	489	69.9
Heleniella sp. (gc, D)	15°	SF	352	0.51	89.0	5.4	0.51	88.4	480	88.9
Thienemannimyia sp. (p, C)	15°	SF	114	0.55	94.9	3.3	0.55	95.2	279	83.6
Tabanidae (p, C)	1°	PB	34	0.51	85.6	15.9	0.64	111.0	80	5.0e
Misc. Chironomidae (gc, D)	15°	PB	18	0.29	50.1	0.8	0.38	66.3	60	75.0[e]
Polypedilum sp. (s, H)	18-	PB	13	0.62	108.2	0.6	0.46	78.9	41	68.6[f]
Chaetocladius sp. (gc, D)	15°	SF	59	0.73	126.4	0.4	0.56	97.7	30	75.0
Empididae (p, C)	15-	PB	8	0.39	68.3	0.4	0.23	39.8	30	75.0[e]
Tipulidae (s, D)	1°	PB	3	0.21	35.9	2.0	0.26	44.3	10	5.0[e]
Dixidae (gc, D)	15-	PB	2	0.28	64.7	0.1	0.29	50.0	8	75.0[e]
TOTAL			2572			248.2			12,687	
GRAND TOTAL			4183			469.0			16,356	

[a] Source of CPI used: ° = derived from growth studies; + = field data and SF distributions; o = literature; - = based upon CPI for similar cited insects (used when other sources were not available).

[b] s = shredder, gc = gathering-collector, fc = filtering-collector, g = grazer/scraper, p = predator; H = herbivore, D = detritivore, C = carnivore

[c] SF = production calculated by the Size-Frequency method.

[d] PB = production calculated by an assumed P/B ratio

[e] Assumed cohort P/B of 5

[f] Assumed annual P/B is the same as derived by SF for this taxon in one of the other study streams.

and environmental stress. CPIs of Chironomidae in SS were estimated as they were in DC. We used Gray's (1981) estimate of a 1-yr CPI and univoltinism for Tabanidae and Tipulidae. Dixidae and Empididae reached maximum sizes similar to many of the midges, and a CPI of 25 d was assumed.

Rattlesnake Springs

EPHEMEROPTERA.—We isolated several *Baetis* sp. larvae in growth chambers in RS to estimate larval development time. These data and field data indicated a CPI of 60 d. *Tricorythodes* sp. were not present in sufficient numbers for an SF production estimate.

ODONATA.—Field data for *Argia tibialis* indicated a CPI of 1 yr.

TRICHOPTERA.—We isolated several *Cheumatopsyche* sp. larvae in growth chambers in RS to estimate larval development time. These data indicated a bivoltine life cycle and a CPI of 6 mo. Because of low densities, field data gave no indication of the CPIs of *Limnephilus* sp. or *Parapsyche* sp.

COLEOPTERA.—Field data provided little indication of the CPIs of beetles because of low numbers.

DIPTERA.—Several *Simulium* sp. larvae were isolated in growth chambers in RS to estimate larval development time. As in SS, we used Gray's (1981) estimate of a 1-yr CPI and univoltinism for Tabanidae and Tipulidae. Dixidae and Empididae grew to maximum sizes similar to many of the midges, and CPIs of 25 d were assumed.

TABLE 6. Annual production (P, mg DW·m^{-2}·yr-1) and percent production of insect functional groups in Douglas Creek, Snively Springs, and Rattlesnake Springs, July 1985 to June 1986.

Functional group	Douglas Creek		Snively Springs		Rattlesnake Springs	
	P	%	P	%	P	%
Grazer/scraper	2651	11.4	0	0.0	0	0.0
Collector						
Gatherer	15,282	65.8	9332	65.9	3621	22.2
Filterer	4198	18.1	3177	22.5	11,800	72.1
(Total)	(19,480)	(83.9)	(12,509)	(88.4)	(15,421)	(94.3)
Shredder	639	2.8	1316	9.3	166	1.0
Predator	449	1.9	329	2.3	769	4.7
GRAND TOTAL	23,219	100.0	14,154	100.0	16,356	100.0

TABLE 7. Annual production (P, mg DW·m^{-2}·yr-1) and percent production of insect trophic levels in Douglas Creek, Snively Springs, and Rattlesnake Springs, July 1985 to June 1986.

Trophic level	Douglas Creek		Snively Springs		Rattlesnake Springs	
	P	%	P	%	P	%
Herbivore	2812	12.1	220	1.6	41	0.3
Detritivore	19,967	86.0	13,605	96.1	15,546	95.0
Carnivore	440	1.9	329	2.3	769	4.7
TOTAL	23,219	100.0	14,154	100.0	16,356	100.0

Functional Group Production

Production by collectors was greatest of all functional groups in all study streams. Collector production was highest in DC, 19.5 g·m^{-2}·yr^{-1}, accounting for 83.9% of the total annual production of insects. In SS and RS, collector production was 12.5 g and 15.4 g, representing 88.4 and 94.3% of the total annual production, respectively. The annual production of all functional groups in each study stream is shown in Table 6.

Trophic Level Production

Herbivores and detritivores are both secondary producers at the same trophic level; carnivores are tertiary producers. For this discussion, we address them separately. Detritivore production was greatest of all trophic levels in each study stream. In DC, detritivore production was about 20.0 g·m^{-2}·yr^{-1}, accounting for 86.0% of the total annual insect production. In SS and RS, detritivore production was 13.6 g and 15.5 g, representing 96.1 and 95.0% of the total annual insect production. Herbivores contributed 12.1% of the productivity in DC, but no other trophic level in any of the three streams was an important contributor to secondary production. The annual production of all trophic levels in each stream is given in Table 7.

DISCUSSION

Interstream Comparisons

DC was clearly the most productive of the three streams studied (Table 6), and this is probably related to the variety of substratum (Table 2) and resulting increase in microhabitat diversity. Minshall (1984) thoroughly reviewed the importance of substratum heterogeneity and its influence on insect abundance and distribution. SS and RS were similar in size and had similar total productivity estimates (Table 6), although important differences existed among the biotic components.

In terms of functional group productivity, collectors dominated in each of the streams. Gatherers were more important in DC and SS, and filterers in RS. The greater filterer/gatherer ratio in RS is probably related to the shifting nature of the sandy substratum (Table 2) and resulting absence of areas for detritus to collect and be harvested. The filtering simuliids occurred on the abundant watercress plants. The scarcity of solid substratum for periphyton development in RS also explains the absence of grazers in this stream. However, substratum composition does not explain a lack of grazers in SS, where solid substratum is present (Table 2).

In SS, the dense riparian canopy almost completely shaded and obscured the stream. This probably prevented the development of a substantial periphytic food base for grazers. In DC, which had both solid substratum and unshaded stream bottom, a significant grazer community was present (Table 6).

Comparing the productivity of taxa common to all three streams shows some differences that are difficult to explain (Table 8). For example, *Simulium* sp. production was similar in DC and SS, but was an order of magnitude greater in RS. This may indicate a richer source of suspended food in RS; however, comparative measurements of this resource were not made. Cushing and Wolf (1982) report a value of 1513 $\mathrm{Kcal \cdot m^{-2} \cdot yr^{-1}}$ of suspended POM in RS, but comparable data are not available for DC and SS. This value is much less than that reported by Minshall (1978) for Deep Creek, a small, cold desert stream in southeastern Idaho. Since *Simulium* sp. production far exceeded that of any other insect in RS (Table 5), competitive exclusion (Hemphill and Cooper 1983) may make it more successful in competing for the limited attachment sites. *Cheumatopsyche* sp. and *Parapsyche* sp., two filtering Trichoptera in RS, had a combined production of 620 mg as compared with *Simulium* sp. production of 11,000 mg. This is a 20-fold difference for organisms of the same functional group. Except for *Simulium* sp., dipteran production was highest in DC for *Chironomus* sp. and Tabanidae, while in SS, production of *Polypedilum* sp. and Tipulidae was highest. Tipulidae production increased by an order of magnitude from RS to DC to SS. This may be related to the relatively high amounts of particulate organic matter (POM) found in the study section of SS (Cushing 1988). Production of *Baetis* sp. is three to four times lower in RS than in the other two streams (Table 8).

TABLE 8. Comparative annual production ($\mathrm{mg\ DW \cdot m^{-2} \cdot yr^{-1}}$) of taxa common to Douglas Creek, Snively Springs, and Rattlesnake Springs, July 1985 to June 1986.

Taxon	Douglas Creek	Snively Springs	Rattlesnake Springs
Ephemeroptera			
Baetis sp.	8317	7012	2542
Odonata			
Argia tibialis	44	139	372
Trichoptera			
Cheumatopsyche sp.	818	1298	486
Diptera			
Simulium sp.	1680	1879	11,175
Chironomus sp.	4920	1386	489
Polypedilum sp.	161	220	41
Tabanidae	130	53	80
Tipulidae	411	1096	10

A likely explanation for some of the differences shown in Table 8 is the winter spates that occur in RS but not in SS or DC. These spates, described by Cushing and Gaines (1989), scour the entire streambed, flushing out accumulated POM and much of the fauna. They occur about every three years and act as a "reset" mechanism because they occur in winter when there are no ovipositing adults, and because they scour and eliminate sources for both upstream migration and downstream drift, they must severely limit the potential productivity of RS. It is notable that the dominant secondary producers in RS are the black flies, organisms that are found in abundance soon after discharge diminishes (Cushing and Gaines 1989).

Intrastream Comparisons

DOUGLAS CREEK.—Secondary production in DC was spread over a wider variety of functional groups (Table 6) and trophic levels (Table 7), even though it was dominated by detritus-feeding collector-gatherers. *Chironomus* sp. and *Baetis* sp. were the dominant secondary producers in the stream.

SNIVELY SPRINGS.—In SS, about 50% of the secondary production was due to *Baetis* sp., a detritus-feeding collector-gatherer; and, as mentioned above, the grazing component was absent. Total dipteran production was of the same order of magnitude as that for *Baetis* sp. but was spread out among several organisms, notably *Simulium* sp., *Chironomus* sp., and Tipulidae (Table 4).

RATTLESNAKE SPRINGS.—Secondary production in RS was less diverse than in the other study streams, with over 68% of the production due to the filtering detritivore *Simulium* sp. The second highest producer was *Baetis* sp., but production was far lower than the black flies (Table 5). The high production of simuliids in RS can be attributed to the presence of multiple cohorts with short development times. Gray (1981) suggested that rapid development may be advantageous in streams subject to spates.

TABLE 9. Comparative whole stream secondary production of insects (P, g DW·m^{-2}·yr-1), except as indicated, in five geoclimatic regions. Streams grouped by geographical region, not by temperature regimes.

Stream	P	S[a]	Fc	Gc	Gr/sc	Pred	Source
Cold/mesic							
Unnamed, Quebec	5.8[b]						Harper 1978
Factory Br., Maine	12.2						Neves 1979
Sand R., Alberta	0.8[c]						Soluk 1985
Caribou R., Minnesota	3.54	0.83	0.62	1.36	0.14	0.59	Krueger and Waters 1983
Blackhoof R., Minnesota	7.13	1.00	3.53	1.15	0.37	1.08	Krueger and Waters 1983
No. Branch Cr., Minnesota	13.23	0.73	5.33	9.43	1.00	2.07	Krueger and Waters 1983
Fort R., Massachusetts	3.3						Fisher 1977
Bear Br., Massachusetts	4.8						Fisher and Likens 1973
L'Ance du Nord, France	12.5	(Total detritivore P = P − Pred.)				2.0	Maslin and Pattee 1981
Bisballe baek, Denmark	26.7					1.3	Mortensen and Simonsen 1983
Humid/mesic							
Satilla R. Georgia[d]	25.2		2.9	18.0		4.3	Benke et al. 1984
Snag substrate[e]	64.8		49.3	8.1		7.5	
Sandy substrate[e]	21.0		0	17.9		3.1	
Mud substrate[e]	17.9		0.2	8.6		9.2	
Cedar R., So. Carolina	3.0	0.1	1.0	1.3	0.02	0.6	Smock et al. 1985
Lower Shope Fk., No. Carolina					1.4		Georgian and Wallace 1983
Upper Ball Cr., No. Carolina							Huryn and Wallace 1987
Bedrock-outcrop	6.1	0.6	2.1	2.1	0.6	0.7	
Riffle	5.6	1.4	0.3	1.8	1.0	1.1	
Pool	7.6	2.4	0.03	3.0	0.3	1.9	
Hot desert							
Sycamore Cr., Arizona	120.9						Jackson and Fisher 1986
New Zealand							
Hinau R.	38.2						Hopkins 1976
Horokiwi R.	41.5						Hopkins 1976
Cold desert							
Deep Cr., Sta. 1, Idaho	1.2						Minshall et al. 1973
Douglas Cr., Washington	23.2	0.6	4.2	15.3	2.7	0.4	This study
Snively Spr., Washington	14.2	1.3	3.2	9.3	0	0.3	This study
Rattlesnake Spr., Washington	16.4	0.2	3.6	11.8	0	0.8	This study

[a] S = shredder; Fc = filtering-collector; Gc = gathering-collector; Gr/sc = grazer/scraper; Pred = predators.
[b] Emergers only.
[c] Only two species of chironomids.
[d] Expressed per unit area of total stream bottom.
[e] Expressed per unit area of habitat

Comparisons with Other Streams

Annual P/B ratios ranged from 3.6 to 121.7 for insects from the study streams. The high annual P/B ratios are attributed to insects with rapid development and multiple cohorts (e.g., many Chironomidae). The annual P/B ratios found in these cold desert spring-streams are generally lower than those reported by Jackson and Fisher (1986) for Sonoran Desert stream insects and by Benke et al. (1984) for southeastern blackwater stream insects. The Sonoran and blackwater streams are warmer and insect development is faster, resulting in a greater number of cohorts. Our annual P/B ratios were generally higher than reported for northern temperate streams (Krueger and Waters 1983), where cooler streams result in insect development at slower rates with fewer cohorts.

Total insect production rates in this study ranged from 14 to 23 g DW·m^{-2}·yr^{-1} and are compared with values for other streams grouped by geographical region (Table 9). Production rates in cold desert streams are well below the higher values found in New Zealand streams, the richer areas (snags) of humid/mesic streams in the southeastern United States, and Sonoran hot desert streams. However, production rates in cold desert streams are higher than those in streams in cold/mesic areas of the United States. These rankings relate to the interaction among stream water temperature, insect development, cohort production intervals, and other factors. However, it should be kept in mind that other factors, e.g., geochemistry, may be influential in governing production as well as temperature. Production values in

Rattlesnake Springs, which has a sandy substratum, are comparable to the sandy areas of the Satilla River in Georgia (16.4 vs 13.1 g DW m^{-2} yr^{-1}, respectively); production of collector-gatherers was identical.

Benke et al. (1984) stated that measurement of secondary productivity of benthic organisms provides a truer indication of their importance in lotic ecosystems than does measurement of either density or biomass. This is intuitively reasonable since measurement of P, a rate, includes consideration of both biomass and density. Our results support the validity of Benke et al.'s (1984) contention. Clearly, our data reveal that collectors are the dominant functional group, and detritivores the dominant trophic level in terms of the secondary productivity of insects in these three streams (Tables 6 and 7). If only biomass or density data are evaluated from these streams (Tables 3, 4, and 5; Gaines et al. 1989), anomalies become evident. Density data in DC reveal that herbivores are equally as numerous as detritivores, but biomass data reveal that detritivores are about two times greater than herbivores. Conversely, when the insects are separated into functional groups, the biomass of grazer/scrapers (herbivores) exceeds that of collectors in DC by a factor of two. Further, collector-filterers in DC represent 18% of the production and 30% of the biomass, but only 7% of the density. In SS, trophic level comparisons reveal that detritivores dominate production, biomass, and density, but if functional groups are compared, biomass data would overemphasize the importance of shredders (30%), which form only 5% of the density and 9% of total production. In RS, the largest anomaly appears when comparing functional groups. Although collector-filterers represent 72% of the total production and 61% of the biomass, their density is similar to the collector-gatherers.

In conclusion, we have found that taxa with short development times and multiple cohorts, such as midges and black flies, are important to cold desert spring-stream production. Previous studies have addressed the difficulties in obtaining accurate field estimates of Simuliidae (black fly) and Chironomidae (midge) larvae CPIs, and thus production estimates (Benke et al. 1984, Behmer and Hawkins 1986, Stites and Benke 1989). Their small size, rapid turnover rate, high density, and diversity make accurate species specific CPI estimates difficult. These same characteristics, however, make midges and black flies very important to stream communities in terms of production. In many streams, they contribute a large percentage of the total community production because of their rapid development and high turnover rates. We found high P/B ratios for simuliids and chironomids, but other investigators have reported similar results (Fisher and Gray 1983, Benke et al. 1984, Stites and Benke 1989). This life-history strategy is particularly advantageous for insects inhabiting the streams that are subjected to severe spates.

Detritus is the major food resource in these small streams; collector-gatherers predominate where there is more substratum diversity (DC and SS), and filterers in systems more prone to the effects of spates (RS). Grazer/scrapers are present whenever suitable substratum and sufficient sunlight are available for development of a periphyton crop. Shredders, surprisingly, are not well represented in these small headwater streams. This may be related to the flushing of the systems by the spates and/or the low amounts of allochthonous detritus reaching the streams (Cushing 1988). Secondary productivity of these cold desert spring-streams was less than that of streams in hot deserts, but generally higher than that in most cold/mesic and humid/mesic streams. Finally, our results underscore the contentions of Benke et al. (1984) that measuring the secondary production of insects in streams provides a better assessment of their role than density or biomass, but the anomalies described above argue for care in applying this generalization to all streams.

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EFFECT OF REARING METHOD ON CHUKAR SURVIVAL

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ABSTRACT.—Survival of adult chukar–imprinted, game farm (sibling/human-imprinted), and wild chukars was compared in three releases (two sites). Combined results indicate similar ($P < .05$) survival for adult-imprinted and wild chukars, but lower rates ($P < .05$) for game farm chukars. With early behavioral conditioning, some potential exists for using captive-reared chukars to establish new populations.

Key words: chukar, chukar rearing, partridge, imprinting, behavior, propagation, survival.

Captive-reared game birds released in the wild generally have poor survival (Csermely et al. 1983, Krauss et al. 1987). A probable reason is behavioral deficiency (Hessler et al. 1970, Roseberry et al. 1987). Hess (1973) reported that imprinting is indispensable for survival of an animal under natural conditions. Thaler (1986) and Dowell (1989) observed improved predator-avoidance behavior of "properly" imprinted game birds. Postnatal visual imprinting as well as embryonic auditory imprinting (Bailey and Ralph 1975) appear to be important. Our objective was to evaluate survival of captive-reared (adult chukar–imprinted vs. conventional game farm–reared) and wild chukars (*Alectoris chukar*).

METHODS AND STUDY AREAS

Adult-imprinted Chukars

Chukar eggs were exposed during the final week of incubation to recorded adult chukar vocalizations. The recordings, from the Cornell Laboratory of Ornithology Library of Natural Sounds, appeared to fit the description of the "rally call" described by Stokes (1961) (recorded vocalizations of incubating or brooding hen chukars were not available).

The brooding facility was a 6.1 × 15.2 × 2.1-m room at the Brigham Young University (BYU) Poultry Research Unit (Provo, Utah). Feed and water were provided through automatic systems, and chukar habitat was mimicked by covering the floor with gravel, small shrubs, grass, and rocks.

Chicks were removed from the incubator within 5 h after hatching and transferred to the brooding facility without allowing exposure to humans. Six adult chukars were released so that the chicks could visually imprint on them.

When four weeks old, the chicks were allowed to access a 5.6 × 22.9 × 2-m outdoor pen. The outdoor pen was visually isolated because of its solid walls and the netting-covered top. Cover was provided by grass, small shrubs, and two deciduous trees.

A hawk model was passed (rope/pulley system) over the pen and a dog introduced twice weekly so chicks could associate adults' alarm calls with predator presence.

Game Farm Chukars

Chukars (same genetic stock as the adult-imprinted birds) were raised at the Utah Division of Wildlife Resources (DWR) Game Farm in Springville, Utah, under conventional methods (brooded in box-type brooders, fed and watered with human contact [sibling/human-imprinted], and moved into flight pens at four weeks of age).

Wild Chukars

Wild chukars were trapped in the Dugway and Thomas ranges, Utah, 3–5 August 1989.

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Release Site I

Antelope Island, located in the Great Salt Lake in Davis County, Utah, varies in elevation from 1282 m to 2010 m. In size it is 24 × 8 km and covers 10,409 ha. Rocky slopes and grassland are the dominant ecological types. Average yearly high and low temperatures are 38.9 and −12.2 C, respectively (Jones 1985). Antelope Island had self-perpetuating and self-sustaining chukar populations until the severe winter of 1983–84, after which no chukars were observed.

On 8 August 1989 (release I), 80 chukars from each group were released, 13 of which were equipped with backpack-mount radio transmitters (Slaugh et al. 1989, 1990). On 2 May 1990 (release III) 65 adult-imprinted, 65 game farm, and 4 wild chukars were released; 9 chukars in each captive-reared group and all 4 of the wild group were fitted with radio transmitters. Radios were attached to every fifth bird captured from the captive-reared groups to reduce bias from ease of capture. All birds were fitted with patagial tags and legbands. Captive-reared chukars were 14 weeks old in release I and 22 weeks old in release III. Wild chukars in all releases were trapped 3–5 August 1989.

Eighteen coyotes (*Canis latrans*) were removed from site I preceding the 1990 release. Mortality data were recorded daily during the first two weeks, then weekly thereafter.

Release Site II

The second study site was the Sterling Hollow/Wind Rock Ridge area of Spanish Fork Canyon. This area ranges in elevation from 1470 m to 3057 m, and the dominant ecological type is mountain brush. Annual precipitation averages between 38.8 cm and 52 cm. Average yearly high and low temperatures are 40 C and −30 C, respectively.

On 25 September 1989 (release II), 11 birds from each group were radio-marked and released at site II. Captive-reared groups were 21 weeks old. Mortality was recorded daily for two weeks, then weekly thereafter.

Statistical Analysis

Data were analyzed using a Product Limit (Kaplan Meier) estimator; a log rank test was used to compare survival curves (Pollock et al. 1989). Only radio-marked birds were compared since their observation was not biased by ease of approach and proximity to release site.

RESULTS

Release I

All adult-imprinted and game farm chukars (both radio and patagial tagged) died within three weeks of release (Fig. 1) with no differences between groups ($P < .05$). Wild birds decreased in number shortly thereafter but experienced higher survival rates ($P < .05$) than captive-reared groups. Coyote predation was the principal cause of mortality.

Release II

There were no significant ($P < .05$) differences (Fig. 1).

Release III

Mortality was similar ($P < .05$) for the adult-imprinted and wild groups but higher ($P < .05$) for game farm chukars (Fig. 1).

All Releases

Combined data for releases I, II, and III indicate similar ($P < .05$) survival for wild and adult-imprinted groups, both having higher ($P < .05$) values than game farm birds (Fig. 1).

DISCUSSION

During release I, wild birds moved quickly to high, rocky areas, whereas captive-reared birds remained at lower elevations and sought cover in the sparse vegetation, where they suffered high mortality. Immediately following demise of captive-reared birds, wild birds began to be killed.

Adult-imprinted and wild birds demonstrated the greatest fear response to human presence, whereas game farm birds tolerated approach. These findings correspond with those of Csermely et al. (1983), who found that red-legged partridges (*Alectoris rufa*) displayed greater fear response toward humans when isolated from them during imprinting. The flightier behavior of the adult-imprinted chukars would likely provide more hunting sport than game farm birds but did not offer sufficient survival advantage under the existing predator pressure.

Adult-imprinted birds apparently had a behavioral advantage over the game farm birds that was not expressed in release I but was demonstrated at release II, apparently due to lower predator pressure. Wild chukar mortality was similar for releases I and II.

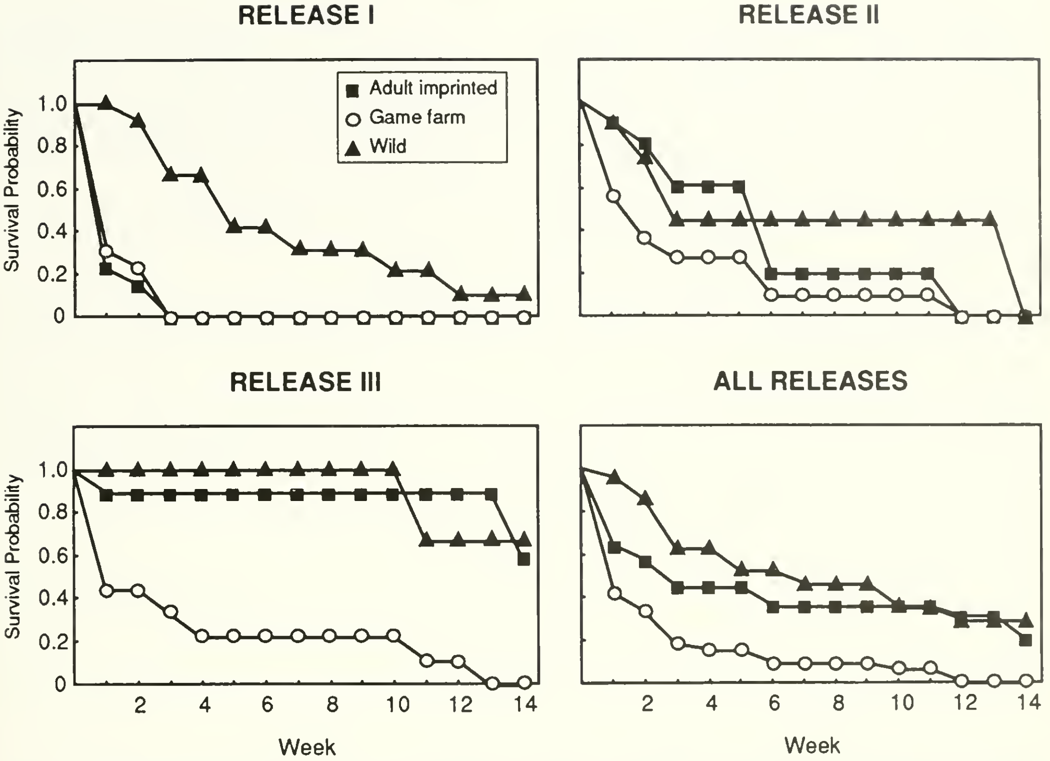

Fig. 1. Chukar survival probability curves: (1) release I (Antelope Island, 8 August–15 November 1989)—no difference ($P < 0.5$) between game farm and adult-imprinted chukars, but both groups are lower than wild chukars; (2) release II (Spanish Fork Canyon, 5 September–12 December 1989)—no differences ($P < .05$) between groups; (3) release III (Antelope Island, 2 May–8 August 1989)—no differences ($P < .05$) between adult-imprinted and wild, but both groups are higher than game farm chukars; (4) all releases—no differences ($P < .05$) between adult-imprinted and wild, but lower for game farm chukars.

Results from release III indicated that survival on Antelope Island for all groups was greater than in the previous year, especially for the adult-imprinted group. The improvement was attributed to predator removal, which may be beneficial even in establishing transplanted wild birds in good habitat. Season of the year may have affected survival, as alternative prey abundance and predator location on the island may have varied. Jonkel (1954), however, observed little difference in chukar survival related to season of release.

Combined data from all releases suggest that captive-reared chukars can be used to establish wild populations if given proper early behavioral conditioning. This study, however, does not provide information on reproductive success.

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DNA EXTRACTION FROM PRESERVED TROUT TISSUES

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ABSTRACT.—We have adapted techniques developed for the extraction of DNA from formalin-fixed, paraffin-imbedded human tissues for use on preserved fish tissues. DNA was successfully extracted and the d-loop region of mitochondrial DNA was amplified with the polymerase chain reaction (PCR). The sequences of the amplified DNA from preserved and modern samples were identical. These techniques were also applied to fin tissue treated with a variety of preservatives. Extraction of DNA from ethyl alcohol and air-dried fin tissues gave yields equivalent to those from frozen tissues. Extraction of DNA from preserved museum specimens of rare or extinct taxa could significantly increase the scope of systematic and phylogenetic studies. Similarly, extraction of DNA from fin tissues provides a nonlethal sampling strategy allowing biochemical systematic analyses of rare or endangered taxa.

Key words: DNA sequencing, polymerase chain reaction, sequencing, cutthroat trout, Oncorhynchus.

As a part of our ongoing studies of the systematics of western salmonids, mainly cutthroat trout (*Oncorhynchus clarki*), we were interested in extracting DNA from preserved fish tissues. Museum collections contain many preserved specimens, usually stored in alcohol but originally fixed in formalin. These could represent a significant reserve of information for systematics research if the DNA could be successfully extracted. In addition, many populations of western trout are in such low numbers that collecting fish for systematic studies could seriously jeopardize their survival. For this reason we also wanted to evaluate the applicability of preserved-tissue DNA extraction techniques to samples of fin tissue. Fin samples could be taken rapidly in the field with minimal stress to the fish. These samples could then be preserved for later DNA extraction.

Medical researchers have developed techniques for the extraction of DNA from formalin-fixed, paraffin-imbedded tissues (Goetz et al. 1985, Debeau et al. 1986). The DNA extracted from these tissues was of sufficient quality that restriction cutting and southern blot analysis were possible (Debeau et al. 1986). DNA has also been successfully extracted from birds held in museum collections, both dried and preserved in 70% ethyl alcohol (Houde and Braun 1988). The DNA extracted from alcohol-preserved birds was significantly degraded (maximum size, 200 base pairs), while that from the dried tissues contained fragments 9–20 kb in length. But even if the DNA obtained with these procedures was degraded, the recent development of the polymerase chain reaction procedure (PCR) (Saiki et al. 1985, 1988, Mullis et al. 1986, Mullis and Faloona 1987, Wong et al. 1987, White et al. 1989) provides a technique to amplify specific fragments of DNA as small as 200 base pairs. These amplified fragments can then be sequenced to decipher genetic relationships (Saiki et al. 1985, Wrischnik et al. 1987, Kocher et al. 1989, Thomas and Beckenbach 1989).

MATERIALS AND METHODS

Archived Specimens

Cutthroat trout collected between 1926 and 1982 and archived in the fish range at the Monte L. Bean Life Science Museum, Brigham Young University, were used to determine the usefulness of the formalin-extraction technique when applied to museum specimens. Samples of liver, muscle, or gut were taken from specimens representing a range of preservation times (Table 1). Tissues were removed from the specimens and placed in 20 volumes of TE9 buffer (500mM Tris, 20 mM EDTA, 10 mM NaCl, pH 9.0; Goetz

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TABLE 1. DNA yields from formalin-fixed museum specimens of cutthroat trout (*Oncorhynchus clarki*). DNA yields were determined using UV spectrometer absorbance readings at 260 nm.

Subspecies	Year	Location	Museum No.	Sample tissue type	Total weight (g)	DNA (µg)	DNA yield (µg/mg tissue)
O. c. bouvieri	1926	Snake R., ID	BYU #26792	liver	0.13	77.5	0.596
O. c. utah	1927	Utah L., UT	BYU #26755	liver	0.64	567.5	0.887
O. c. utah	1940	Utah L., UT	BYU #26756	liver	0.65	310.0	0.477
O. c. utah	1982	Deaf Smith, UT	BYU #176896	muscle	0.24	147.5	0.615
O. c. utah	1982	Deaf Smith, UT	BYU #176890	gut	0.42	965.0	2.298
O. c. utah	1928	Trout Cr., UT	BYU #26858	liver	0.07	51.0	0.728
O. c. utah	1984	Deep Cr., UT	BYU #176793	muscle	0.11	57.5	0.523

et al. 1985). The buffer was changed twice over 24 hours.

Fin Tissues

Fin tissues were taken from anesthetized hatchery rainbow trout (*Oncorhynchus mykiss*) that ranged in length from 15 to 25 cm. Samples were taken from all fins but were restricted to the outer edges of the fins to more accurately represent the region that would be sampled in the field. Approximately 1 cm^2 of fin was removed for each sample. These were placed in labeled 1.8-ml polyethylene tubes with gasketed screw caps. Four samples were taken for each of six treatments applied to the fins. These were (a) 10% formalin, (b) 40% isopropyl alcohol, (c) storage in a standard freezer at −20 C, (d) storage in an ultracold freezer set at −80 C, (e) 70% ethyl alcohol (EtOH), and (f) air-drying. The samples were held in the tubes for 45 days, after which the preservatives were decanted and the tissues soaked in TE9 for 24 hours, with no change in the buffer. The frozen and air-dried samples were not soaked in buffer prior to extraction. One sample stored at −20 C was lost during storage.

Extraction Procedure

Tissue samples were minced with a clean razor blade (to 2 mm or less in cross section) and placed in 15-ml centrifuge tubes with 10 ml of TE9 and 0.1 g of SDS. Five mg of proteinase K was added to each sample, and the tubes were capped and incubated in a shaking water bath for 24 hours at 55 C. An additional 5 mg of proteinase K and 0.1 mg SDS were added to each sample and the tubes returned to the shaking water bath for 50 hours at 55 C to remove residual undigested tissue. The samples were transferred to 30-ml tubes, and an equal volume of phenol-chloroform was added to each. The tubes were inverted several times to mix and then centrifuged in an SS-34 rotor at 10,000 rpm for 10 minutes. The aqueous phase from each sample was removed with an inverted glass pipette and placed into clean 30-ml tubes and the procedure repeated. A final extraction of the aqueous phase was made with one volume of chloroform and centrifuged as before. The aqueous phase from each sample was transferred to a new tube and .1 volume of 3 M sodium acetate solution added. The mixtures were precipitated with one volume of 95% EtOH and stored at −20 C overnight (12 hours minimum). Each sample was centrifuged at 10,000 rpm for 10 minutes and the supernatant carefully poured off, leaving a DNA pellet. The pellets were washed with 70% ethyl alcohol and centrifuged again for 10 minutes at 10,000 rpm. The alcohol was poured off and the samples allowed to air dry. The pellets were resuspended in a 3 mM Tris, 0.2 mM EDTA solution (pH 7.2). RNase was added to a final concentration of 20 µg/ml.

RESULTS AND DISCUSSION

Archived Specimens

Muscle and liver tissues yielded comparable amounts of DNA, and exceptionally high yields were obtained from the sample of gut tissue (Table 1). Because the gut tissue was washed in buffer immediately after removal from the preserved specimen, contamination from items in the alimentary canal should have been minimal. Gut tissue was easily digested, indicating a relatively rapid release of DNA (Dubeau et al. 1986), and this could have been associated with the high yields. DNA samples (20 µl) from the museum specimens were electrophoresed on a

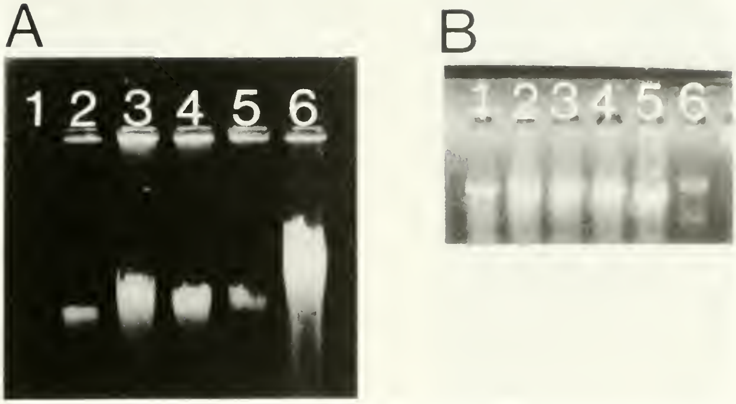

Fig. 1. DNA electrophoresed on 1% agarose gels after being extracted (Fig. 1A) from formalin-preserved museum specimens and following PCR amplification (Fig. 1B). The DNA from the trout collected in 1926 (liver) is only faintly visible (lane 1, Fig. 1A). The DNA from 1927 (liver), 1940 (liver), 1982 (muscle), and 1982 (gut) are in lanes 2–5, respectively. The DNA in lane 6 was extracted from a contemporary frozen liver sample. The PCR products are shown in Figure 1B. Lanes 1–6 in Figure 1B correspond to the DNA templates shown in lanes 1–6 in Figure 1A.

TABLE 2. A comparison of the nucleotide sequence (120 base pairs) from the SD-1 region of the mitochondrial DNA d-loop. The DNA was amplified with the polymerase chain reaction. The top row represents the base sequence from frozen-tissue DNA, and the lower row represents the sequence from a formalin-preserved specimen. The frozen-tissue specimen (BYU #90621) is *O. c. utah*, from McKinzie Creek, UT, collected 8-17-88. The preserved-tissue specimen (BYU #26755) is *O. c. utah*, from Utah L., UT, collected in 1927. Both vouchers are archived in the fish range at the Monte L. Bean Life Science Museum.

Frozen	AAGGCTATCC	TTAAGAAACC	AGCCCCTGAA	30
Preserved	AAGGCTATCC	TTAAGAAACC	AGCCCCTGAA	
	AGCCGAAGTA	AAGCATCTGG	TTAATGGTGT	60
	AGCCGAAGTA	AAGCATCTGG	TTAATGGTGT	
	CAATCTTATT	GCCCGTTACC	CACCAAGCCG	90
	CAATCTTATT	GCCCGTTACC	CACCAAGCCG	
	GGCTTCTCTT	ATATGACTAG	GGCCTCTCCC	120
	GGCTTCTCTT	ATATGACTAG	GGCCTCTCCC	

1% agarose gel containing ethidium bromide (Fig. 1A) to verify extraction. The DNA samples extracted from fresh and preserved tissue samples were used in a PCR reaction (25 μl total volume) using primers for the d-loop region of trout mitochondrial DNA developed by K. Thomas (University of California, Berkeley), with standard conditions (Perkin Elmer Cetus, Norwalk, Connecticut). Cycle times and temperatures were 1 minute at 92 C, 1 minute at 53 C, and 2 minutes at 72 C, for 35 cycles. PCR products are shown in Figure 1B. DNA extraction controls containing no fish tissue did not yield PCR products under identical conditions (data not shown). Subsamples of the PCR products from preserved and fresh tissue samples were sequenced (Fig. 2) and compared with contemporary sequence data from cutthroat trout (Table 2). The sequence data were identical, indicating that within the amplified segment no base modifications had occurred in the formalin-preserved sample.

Fin Clips

We obtained DNA from all fin clips regardless of preservation method. Mean yields ranged from a low of 0.40 μg/mg of tissue from formalin-preserved fin clips to a high of 1.104 μg/mg in air-dried samples (Table 3). The treatment effects were examined with analysis of variance (Table 4), and a highly significant difference was found between the treatments. Fisher's least significant difference multiple comparison procedure was applied to separate those treatment

Fig. 2 (at left). Sequence gel from a portion of the mitochondrial DNA d-loop. Column A is the sequence for a contemporary sample of trout DNA (BYU #90621) and column B is the sequence from a preserved trout specimen (BYU #26755) collected in 1927. The sequence gel is read from the bottom up, and the columns represent guanine (G), adenine (A), thymine (T), and cytosine (C), respectively.

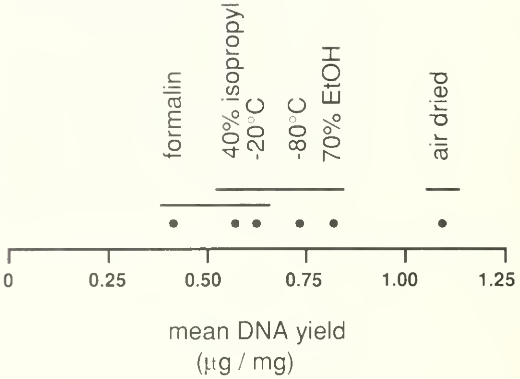

Fig. 3. Multiple comparisons of the means of the six fin tissue treatments, using Fisher's least significant difference test (alpha = 0.01). Lines connect means that do not differ significantly from one another.

TABLE 3. DNA yields from fin tissue preserved with different methods. The fin clips, approximately 1 cm^2 each, were taken from hatchery-reared rainbow trout (*Oncorhynchus mykiss*). DNA yields were determined using UV spectrometer absorbance readings at 260 nm.

Preservation method	N	Mean yield (µg/mg)	Standard deviation
formalin	4	0.402	0.15743
40% isopropyl	4	0.569	0.19111
-20 C	3	0.644	0.10016
-80 C	4	0.740	0.06295
70% EtOH	4	0.822	0.07964
air-dried	4	1.104	0.13443

groups that differed significantly from one another. These comparisons (Fig. 3) indicate that the air-dried treatment gave yields significantly higher than the other treatments. Because the weights used in calculating the DNA yields were the preextraction values and not the pretreatment weights, the initial weights (predrying) of the air-dried samples are not known. However, based on the initial size of the fin clips, they are assumed to have been similar. While air-drying yields are much better than

TABLE 4. One-way analysis of variance of the fin clip treatment effect on DNA yield

Source	Degrees of freedom	Sum of squares	Mean square	F	Prob > F
Treatment	5	1.14512	0.22902	13.47	0.0000
Error	17	0.28911	0.01700		
Total (adj)	22	1.43424			

those resulting from other preservation methods, the lack of preservatives could allow secondary contamination of samples through bacterial or fungal colonization, and air-drying probably should not be used in collecting samples in humid areas or where adequate storage is not possible. The yields obtained from ethyl alcohol preservation are equal to those from frozen tissues and superior to both isopropyl alcohol and formalin preservation. Of the preservatives examined in this study, ethyl alcohol would appear to be the preservative of choice in most field situations. This eliminates the necessity of carrying dry ice or liquid nitrogen into the field to preserve tissues. Other preservative solutions should be considered; for instance, Seutin, White, and Boag (1991) reported successful DNA extraction from avian tissues preserved in a mixture of EDTA, NaCl, and DMSO.

CONCLUSIONS

The ability to extract, amplify, and sequence DNA from formalin-preserved museum specimens increases the information value of museum holdings. In addition to being a record of morphological and meristic information, the specimens can be used in biochemical studies. Because museum collections include type specimens, rare species, and representatives of now extinct forms, many key phylogenetic relationships can be reexamined. The extraction techniques can be applied to contemporary preserved tissues as well. Fin tissues give adequate yields with this technique for both restriction enzyme digestion and PCR amplification. Fin samples, which can be taken nonlethally, present opportunities to examine fish populations that would otherwise be inaccessible to tissue collection because of management considerations.

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RELATING SOIL CHEMISTRY AND PLANT RELATIONSHIPS IN WOODED DRAWS OF THE NORTHERN GREAT PLAINS

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ABSTRACT.—Soils of the green ash/chokecherry habitat type in northwestern South Dakota were evaluated for 22 properties to determine whether any could be correlated with density of chokecherry (*Prunus virginiana*) and snowberry (*Symphoricarpos occidentalis*). Surface soils were moderately fertile, with high levels of all elements except phosphorus and nitrogen. Soils were fine textured, with moderately high cation exchange capacity and saturation percentages. However, soils were nonsaline-nonalkaline with low amounts of exchangeable sodium. None of the soil properties showed good correlation with chokecherry and snowberry densities. Greatest correlations were found between each of the shrub species and grass.

Key words: wooded draws, green ash, shrubs, Prunus virginiana, Symphoricarpos occidentalis, *grazing.*

Wooded draws constitute a valuable habitat type in the northern Great Plains. They provide shelter from wind and weather and contain greater moisture than surrounding areas, resulting in an abundance of plant life and forage. An understanding of soil-plant relationships of these wooded draws has become more critical since these areas have been observed to be in decline (Boldt et al. 1978) for a variety of reasons (Girard et al. 1987).

Studies that correlate habitat type with soil properties are particularly useful in efforts to manage these systems. Knowledge gained from such studies might help managers determine the potential habitat type of a site after vegetation decimation. Efforts and limited resources could then be concentrated on sites with the greatest potential for rehabilitation.

This study was conducted to characterize the surface soil chemistry of the green ash/chokecherry (*Fraxinus pennsylvanica/prunus virginiana*) habitat type in northwestern South Dakota and to relate these soil properties as well as grass cover to density of chokecherry and snowberry (*Symphoricarpos occidentalis*). This habitat type is considered a topographic climax (Hansen, Hoffman, and Steinauer 1984, Hansen and Hoffman 1988) and is one of the most important in the northern Great Plains.

STUDY AREA

The study area is approximately 5 miles northwest of Bison, South Dakota, in Perkins County on lands administered by the USDA Forest Service, Custer National Forest. Geology of the area has been described by Hansen (1985). The topography is rolling to steep plains dissected by streams and drainageways. The climate of the area is characterized by warm summers and very cold winters. Annual precipitation averages 36 cm, with most received in the spring and summer.

The habitat types of the area have been described by Peterson (1987). The green ash/chokecherry habitat type was found on shallow to moderately deep, well-drained, Cabba-Lantry loam soils of upland ridges and the sides of steep drainageways with slopes of 15% to 40%.

METHODS

Collection of Samples

Soil samples were collected during the summer of 1986 from 24 green ash/chokecherry draws spaced over a 2769-ha pasture. The vegetation of the 24 wooded draws ranged from few trees and shrubs to a dense overstory and understory of trees and shrubs. Sampling was conducted

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TABLE 1. Chemical properties of soil samples collected from green ash/chokecherry habitat type near Bison, South Dakota ($n = 72$).

Soil	Mean	Range	Standard deviation
pH	7.3	6.3–7.8	0.3
EC (mmhos/cm)	0.6	0.4–2.6	0.3
Organic matter (%)	9.1	4.2–19.8	3.3
NO_3-N (µg/g)	3.1	1.0–17.0	2.6
P (µg/g)	2.5	0.1–10.5	2.2
K (µg/g)	321	202–491	67
Zn (µg/g)	3.4	0.9–9.2	2.0
Fe (µg/g)	21.2	6.9–268.0	31.5
Mn (µg/g)	7.6	3.2–24.1	3.4
Cu (µg/g)	2.1	0.8–5.6	0.8
Ca (meq/l)	4.5	2.0–20.8	2.3
Mg (meq/l)	2.1	1.0–12.5	1.4
Na (meq/l)	0.2	0.1–0.9	0.1
SAR	0.1	0.1–0.2	0.1
Saturation (%)	72.9	48.8–106.5	11.2
CEC (meq/100 kg)	45.2	29.9–62.4	7.6
Ext.[1] Ca (mg/kg)	4311	2580–6830	937
Ext. Mg (mg/kg)	684	90–987	171
Ext. Na (mg/kg)	15.2	1.8–57.5	7.7
Sand (%)	32.9	20–67	9.1
Silt (%)	40.8	21–51	5.4
Clay (%)	26.3	11–40	6.2

[1] Extractable cation.

at three locations in each draw. At each location (approximately 250 m^2 in area), three frames (20 × 50 cm) were randomly located. Stem densities of chokecherry at these locations ranged from low (0–2 stems/frame), to medium (3–6 stems/frame), and high (greater than 8 stems/frame). All stems were counted within a frame and the three values averaged for each location. Canopy cover of grass was estimated in each frame (Daubenmire 1959). One soil sample was collected within each frame to a depth of 10 cm. The three soil samples from each location were combined for chemical analysis, yielding a total of 72 samples.

Soil Analyses

Amounts of soil elements (P, K, Zn, Fe, Mn, Cu) were determined by using the ammonium bicarbonate–diethylenetriamine pentaacetic acid (AB-DTPA) extract (Soltanpour and Schwab 1977) and inductively coupled plasma atomic emission spectrometry (ICP-AES) (Jones 1977). The AB-DTPA procedure was developed and is used by the Colorado State University Soil Testing Laboratory. An equal amount of potassium is extracted as with the ammonium acetate test (Knudsen et al. 1982), and the same amount of iron is extracted as with the standard DTPA test (Havlin and Soltanpour 1981). Half as much phosphorus is extracted using AB-DTPA as in the sodium bicarbonate extract (Olsen et al. 1954), and slightly less zinc is extracted than in the standard DTPA test (Havlin and Soltanpour 1981). AB-DTPA extractable copper and manganese are highly correlated with DTPA-extractable levels of these elements (r^2 = .75 and .86, respectively) (Soltanpour and Schwab 1977).

The pH was measured with a pH meter that used a combination electrode on a saturated paste. Sodium adsorption ratio (SAR) was estimated from levels of soluble calcium, magnesium, and sodium measured in a saturation extract by means of ICP-AES. Total soluble salts were measured on the filtered extract with a solubridge.

Organic matter was determined by wet oxidation with spontaneous heat of reaction. Potassium dichromate and concentrated sulfuric acid were used for organic matter, and results were determined calorimetrically. Nitrate nitrogen was determined by the chromotropic acid method. Levels of extractable Ca, Mg, and Na were measured by using ICP-AES on an ammonium acetate extract. Cation exchange capacity was determined by the sodium saturation method (Page 1982).

Statistical Analyses

Simple linear regression was used to relate soil chemistry variables to chokecherry and snowberry densities; the points were plotted to check for nonlinear relationships. Stepwise regression was used to test relationships between soil chemistry, canopy cover of grass, and density of each shrub. The regression model $Y=a+bx^c$ provided the best fit in relating chokecherry and snowberry densities with canopy cover of grass. Soil variables and densities of both shrubs were subjected to a nonhierarchical cluster analysis (ISODATA) to group the sites (Ball and Hall 1967). Stepwise discriminant analyses were used to estimate compactness of clusters and identify the key variables that accounted for their differences. However, cluster analyses and discriminant analyses and simple correlation plots did not provide any meaningful results.

RESULTS AND DISCUSSION

Nitrate nitrogen levels averaged 3.0 µg/g and ranged from 1.0 to 17.0 µg/g (Table 1). Soil organic matter ranged from about 4% to nearly 20%. These values compare well with values from surface soil samples from hardwood forest on fine-textured soils (Charley 1977). Organic matter levels ranged substantially higher than those from soils from similar sites in North Dakota (Hansen, Hoffman, and Bjugstad 1984), Montana, and South Dakota (Hansen and Hoffman 1988). Nitrate levels appeared adequate for growth of rangeland plants (Soltanpour et al. 1979).

Soils were near neutral in pH (Table 1) and similar to other sites in Montana, North Dakota, and South Dakota (Hansen, Hoffman, and Bjugstad 1984, Hansen and Hoffman 1988). Availability of nutrients at this pH is near maximum except for Fe, Mn, Zn, and Cu, which become less available above pH 7.0 (Brady 1974). Plants usually grow well between pH 5 and 8.5 (Donahue et al. 1977) if no other growth factor is limiting. Phosphorus and potassium content averaged 2.5 µg/g and 321 µg/g, respectively. Thus, phosphorus levels were low, whereas potassium, zinc, copper, and manganese levels were high (both generally and relative to similar sites in the northern High Plains [Hansen, Hoffman, and Bjugstad 1984, Hansen and Hoffman 1988]). Iron levels averaged 21.2 µg/g and were fairly high.

The cation exchange capacity (CEC) was rather high at 45.2 meq/100 kg (Table 1). Clays in these soils are likely to have high adsorptive capacities since organic matter content and clay content did not fully account for the high CEC (Brady 1974). The sodium adsorption ratio (SAR) indicated minimal saturation of the exchange complex by sodium. Electrical conductivity was low at 0.6 mmhos/cm. These soils would be classed as nonsaline-nonalkaline with low electrical conductivity and exchangeable sodium percentage. The saturation percentage at 72.9 was somewhat higher than other nonsaline-nonalkaline soils in this classification (Richards 1954). The soil moisture percentage at 15 MPa, which is approximately equivalent to the wilting percentage, was 18%. These soils are thus relatively fine textured on average. Sand, silt, and clay averaged 33%, 41%, and 26%, respectively.

Soluble Ca, Mg, and Na were 4.5, 2.1, and 0.2 meq/l, respectively (Table 1). Extractable Ca, Mg, and Na averaged about 4311, 684, and 15 mg/kg, respectively. These corresponded to 10.8, 5.7, and 0.065 meq/100 g soil and exchangeable percentages of 23.8, 12.6, and 0.1, respectively. Thus, of these elements, Ca was predominant on the exchange complex, and exchangeable Na was very low. However, calcium was low relative to comparable sites of vegetation and landscapes (Hansen, Hoffman, and Bjugstad 1984, Hansen and Hoffman 1988).

Simple correlation coefficients for density of either chokecherry (r = .26 to −.18) or snowberry (r = .36 to −.20) with various soil properties were low (Table 2). Twelve soil properties were negatively associated with chokecherry density. Phosphorus showed the greatest positive relationship with chokecherry density (r = .26). Only four soil variables (pH, P, extractable Ca, and CEC) were negatively correlated with snowberry density. Magnesium showed the highest correlation with snowberry density (r = .36). Soil properties varied some for both species at the microsite level but were not statistically different (p < .10). For example, when density of chokecherry was high (no snowberry), phosphorus was somewhat greater than phosphorus on sites with high snowberry densities (no chokecherry), and thus, a positive correlation.

Stepwise multiple regression using all soil properties with either chokecherry or snowberry stem density did not provide meaningful results. However, a good relationship was found

TABLE 2. Simple correlation coefficients for densities of chokecherry and snowberry with chemical properties of soil of green ash/chokecherry habitat type near Bison, South Dakota (n = 72).

Soil	Chokecherry	Snowberry
pH	0.19°	0.20°
EC	0.16	0.28°°
Organic matter	−0.17	0.15
NO_3-N	0.03	0.10
P	0.26°°	−0.06
K	0.14	0.18
Zn	−0.13	0.23°°
Fe	0.11	0.03
Mn	0.03	0.23°°
Cu	0.07	0.09
Ca	−0.18	0.25°°
Mg	0.17	0.36°°
Na	0.09	0.30°°
SAR	0.08	0.08
Saturation	0.10	0.10
Ext.[1] Ca	0.02	0.16
Ext. Mg	0.01	0.23°°
Ext. Na	−0.13	0.17
CEC (meq/100 kg)	0.04	−0.02

*Significant at α = .05

**Significant at α = .01

[1] Extractable cation

for predicting chokecherry density using snowberry density and canopy cover of grass (Table 3). Predicting snowberry stem density using chokecherry density and grass cover similarly showed a good relationship (r^2 = .50). When snowberry stem density was high, chokecherry stem density was low and vice versa (Fig. 1). Chokecherry density showed a good relationship (r^2 = .48) with canopy cover of grass (Fig. 1). Stem densities of chokecherry were greatest when canopy cover of grass was low.

Overall, soil properties were not highly correlated with either chokecherry or snowberry stem density. Each shrub was more influenced by the density of the other or the amount of grass cover. Factors such as other shrubs, trees, disease, fire, soil compaction, and grazing may also influence stem density of both chokecherry and snowberry (Boldt et al. 1978, Severson and Boldt 1978, Uresk and Paintner 1985, Uresk and Boldt 1986, Uresk 1987), but these factors were not considered in the present study.

SUMMARY

Surface soils of the green ash/chokecherry woodland in northwestern South Dakota near Bison were found to be moderately fertile with fairly high levels of nutrients except phosphorus, which was low, and nitrogen, which was moderately low. Organic matter ranged from about 4% to 20%. These soils were fine textured with moderately high cation exchange capacity and saturation percentages. They were classed as nonsaline-nonalkaline with low amounts of exchangeable sodium.

Soil properties showed low correlation relationships with chokecherry or snowberry stem density. A good relationship was found between the two species of shrubs and grass. Additional factors such as density of other shrubs or trees, disease, fire, soil compaction, and grazing may also influence densities of chokecherry or snowberry and interact with soil surface properties.

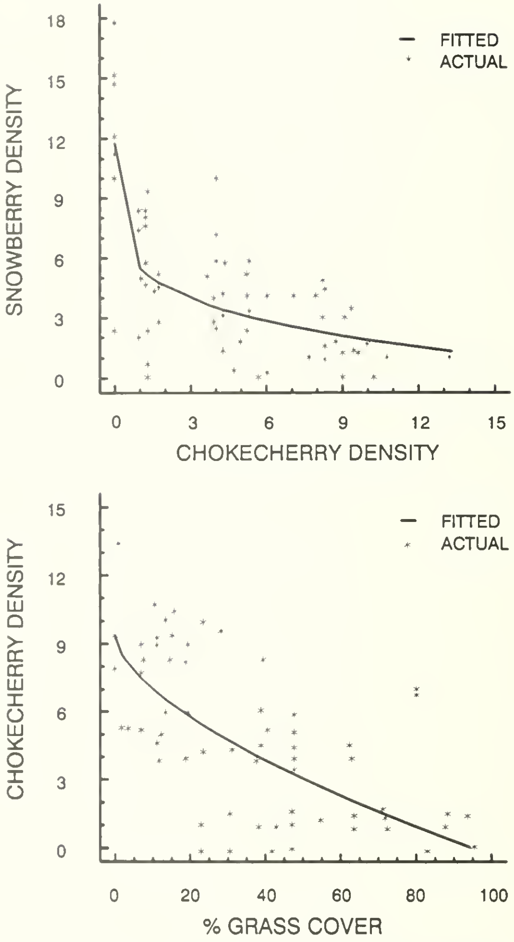

Fig. 1. Snowberry stem density (stems/0.1 m^2) is greatest when chokecherry stem density is the least, but decreases as chokecherry density increases. Chokecherry stem density is greatest when grass cover is the least, and density decreases as grass cover increases.

TABLE 3. Coefficients (a, b, and c), standard error of the estimate (SE), and correlation (r^2) describing relationships of chokecherry (C), snowberry (S), and grass (G) in green ash/chokecherry habitat type (n = 72).

Density (Y)	a	b	b	c	SE	r^2	Type[1]
Chokecherry	9.651	−0.488S	−0.082G		1.84	0.72	S
Snowberry	11.694	−1.076C	−0.076G		2.66	0.50	S
Snowberry	11.758	−6.266C		0.197	2.51	0.55	E
Chokecherry	9.323	−0.555G		0.620	2.53	0.48	E

[1] S = stepwise regression ($Y = a+bx^1+bx^2$); E = exponential regression ($Y = a+bx^c$).

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THE GENUS *ARISTIDA* (GRAMINEAE) IN CALIFORNIA

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ABSTRACT.—The taxonomy of *Aristida* (Gramineae) in California is revised. The genus is represented in the state by six species and 11 taxa. Identification keys, descriptions, selected synonymy, distribution records, and illustrations are provided.

Key words: Aristida, *floristics, California.*

As part of the current revision of Willis Lynn Jepson's A Manual of the Flowering Plants of California (1923), sponsored by the Jepson Herbarium of the University of California at Berkeley, an examination of the taxonomy, nomenclature, and distribution of the California species of *Aristida* was undertaken. Jepson (1923) originally listed 10 species of *Aristida* for California, and subsequent floristic endeavors increased this number to 12, reported by Munz and Keck (1968). This work treats six species apportioned to 11 total taxa.

Aristida are peculiar in the development of the fusiform, indurate floret. The lemma (in North American species) is convolute and completely encloses the palea and flower, forming a rather firm anthoecium, or flower casing. This configuration customarily prevents the exsertion of anthers and stigmas, resulting in cleistogamous (and self-pollinated) reproduction. However, in some spikelets of *A. purpurea* Nuttall, *A. divaricata* Humb. & Bonpl. ex Willenow, and other species, swelling of the lodicules will often spread the lemma and palea, and the anthers and stigmas are commonly exserted from the anthoecium during and after anthesis, evidence of possible cross-pollination. In *A. dichotoma* Michaux of central and eastern United States, two kinds of flowers are developed: one with three anthers each 2–3 mm long, presumably adapted for chasmogamous reproduction, and the other with a single anther less than 0.3 mm long (personal observation). The smaller anther is always found retained within the floret and apparently functions in cleistogamous reproduction. This condition is also reported for *A. oligantha* Michaux (Henrard 1929).

The tip of the lemma often bears a column or beaklike structure in species of Aristida, and two terms describe this condition. An awn column is formed by the connivent or coalescent, often twisted bases of the awns above the lemma. This is a relatively uncommon arrangement but is seen in Aristida californica Thurber. A *beak* of the lemma, however, is sometimes formed by the lemma apex. It is often narrow and twisted, as in *A. divaricata* and *A. purpurea*. The term *awn*, as used herein, refers to the free portion only and is measured from the summit of the beak or awn column to the tip of the awn.

North American *Aristida* have been classified in three different sections of the genus: *Arthratherum*, *Streptachne*, and *Aristida* (*Chaetaria*) (Henrard 1929, Clayton and Renvoize 1986). In section *Arthratherum*, the lemma body is terminated by an awn column that disarticulates from the rest of the floret. This section is represented in California by *A. californica*. The section *Streptachne* is characterized by the extreme reduction of the lateral awns, illustrated consistently in *A. ternipes* Cavanilles, but also found in other species that are not usually placed in this section, such as *A. adscensionis* Linnaeus. In a study of *Aristida* species affiliated with *A. divaricata*, Trent (1985) found that some degree of reduction of the lateral awns was a common occurrence in numerous species, and concluded that this feature was often not a good indicator of biologic relationship. The validity of the section *Streptachne* based on this criterion is doubtful. Section *Aristida* comprises the remaining California species without articulation in the lemma or consistent reduction of lateral awns.

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Because the sectional classification of the genus remains largely unexamined and unsatisfactory, for this report the California species are sorted into informal "groups." These groups do not necessarily correspond to any formal rank but parallel those used by Hitchcock and Chase (1951) and Allred (1986).

GROUP ADSCENSIONES.—*Aristida adscensionis*, characterized by the annual habit, branching at the upper nodes, and erect awns.

GROUP DICHOTOMAE.—*Aristida oligantha*; characterized by the annual habit, branching at the upper nodes, and a tendency for the central awn to coil.

GROUP DIVARICATAE.—*Aristida divaricata* and *A. ternipes*; characterized by the stiffly spreading primary (and often secondary) branches with axillary pulvini. These two species are usually placed in different sections of the genus (*Aristida* and *Streptachne*, respectively).

GROUP PURPUREAE.—*Aristida purpurea*, including seven varieties; characterized by generally unequal glumes, a narrowed beak of the lemma, and generally erect branches; merges with the Divaricatae through *A. purpurea* var. *parishii* (Hitchcock) Allred, as well as *A. pansa* Wooton & Standley of the Chihuahuan Desert.

GROUP TUBERCULOSAE.—*Aristida californica*; characterized by the disarticulation of the awns and awn column from the body of the lemma.

Following are identification keys to all taxa, descriptions based on California specimens, counties of occurrence in California, lists of selected specimens examined, and an illustration of each taxon. Herbaria are abbreviated according to Holmgren et al. (1981). Updated information on the distribution of *Aristida* in California will be welcomed by the author.

Aristida Linnaeus, Sp. Pl. 82. 1753.

Tufted annuals or perennials; *culms* generally erect, the internodes mostly semisolid. *Sheaths* open. *Ligules* a ring of hairs. *Blades* flat to involute, lacking auricles. *Inflorescence* generally a panicle, occasionally racemose or spicate. *Spikelets* 1-flowered, disarticulating above the glumes. *Glumes* equal to very unequal, thin, membranous, 1- to 7-nerved, often as long as the floret or longer. *Lemma* 3-nerved, terete, indurate at maturity and enveloping the palea and flower; *callus* oblique, usually sharp-pointed and bearded; *awns* 3 in number, terminal on the lemma, the lateral awns sometimes reduced or obsolete. *Palea* 2-nerved, thin, shorter than the lemma. *Lodicules* 2. *Stamens* 1 or 3. *Caryopsis* enclosed in the anthoecium, fusiform, the hilum scar linear, the embryo small. $X = 11$.

Key to the Genus *Aristida*

1. Culm internodes and nodes conspicuously hairy . . . . *A. californica* var. *californica*

— Culm internodes and nodes glabrous 2

2(1). Plants annual, generally much branched above the base 3

— Plants perennial, simple or only weakly branched above the base 4

3(2). Central awns mostly 3–7 cm long . . . *A. oligantha*

— Central awns mostly 0.7–2 cm long . *A. adscensionis*

4(2). Primary panicle branches erect to spreading or drooping, but at least the bases of the branches appressed to the main axis, without pulvini in the branch axils . . . . *A. purpurea*

— Primary panicle branches abruptly spreading from the main axis with pulvini in the branch axils . . . 5

5(4). Lower panicle branches ascending, the upper branches appressed . . . . *A. purpurea* var. *parishii*

— Lower and upper panicle branches spreading . . . 6

6(5). Anthers 0.8–1 mm long; summit of lemma twisted at maturity; base of blade glabrous above the ligule . . . . *A. divaricata*

— Anthers 1.2–3 mm long; summit of lemma not or only slightly twisted at maturity; base of blade with scattered pilose hairs above the ligule . *A. ternipes*

Aristida adscensionis Linnaeus, Sp. Pl. 82. 1753. SIX WEEKS THREEAWN (Fig. 1) [*A. adscensionis* var. *abortiva* Beetle, *A. adscensionis* var. *decolorata* (Fournier) Beetle, *A. adscensionis* var. *modesta* Hackel]. Tufted and generally annual, but extremely variable in size, growth habit, and longevity; *culms* erect to geniculate, simple to much-branched, (3)10–50(80) cm tall; *internodes* glabrous. *Sheaths* generally shorter than the internodes. *Ligules* 0.4–1 mm long. *Blades* flat to involute, 2–14 cm long, 1–2.5 mm wide. *Panicle* narrow and contracted, 5–15(20) cm long, often interrupted below, the spikelets aggregated on short branches. *Glumes* unequal, 1-nerved, the first 4–8 mm long, the second 6–11 mm long. *Lemmas* 6–9 mm long, slightly flattened, scabrous on the midnerve; *awns* flattened at the base, spreading, the central awn 7–18(23) mm long, the lateral awns somewhat shorter, rarely 0–2 mm long. *Palea* 0.5–1 mm long, hyaline, blunt, fan-shaped. *Anthers* 0.3–0.7 mm long. *Caryopsis* somewhat shorter than the lemma. $2n = 22$. Dry, open places and rocky hills below

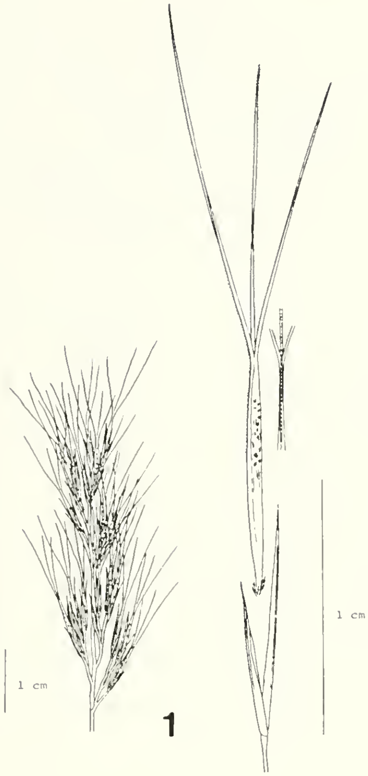

Fig. 1. *Aristida adscensionis*, inflorescence and spikelet.

1000 m. COUNTIES: Imperial, Inyo, Los Angeles, Riverside, San Bernardino, San Diego, San Luis Obispo, Santa Barbara.

Aristida adscensionis ranges in habit from small, unbranched plants scarcely 3 cm tall with only one or two spikelets to large, much-branched clumps 80 cm tall with numerous branches and spikelets. Several varieties have been named based on differences in plant and panicle size, degree of branching, and the development of the awns. Variation in size and robustness seems related to precipitation, and populations at the same site may vary drastically from year to year. The validity of reduced lateral awns as a taxonomic character is also questionable. Most species of *Aristida* have forms with the lateral awns reduced, and this seems to occur almost indiscriminately and without any correlation with other features.

SELECTED SPECIMENS.—**Imperial Co:** rd from Ogilby to Blythe, 17 Feb 1958, Bacigalupi, R. 6136 [JEPS]; Carriso Mts, Painted Gorge, 17 May 1938, Ferris, R. S. 9622 [UC]; near Dixieland, 13 Oct 1912, Parish, S. B. 8239 [JEPS]. **Inyo Co:** Panamint Mts, Death Valley, 18 Apr 1978, Dedecker 4541 [UC]; 11 mi W of Death Valley, 28 Mar 1947, Keck, D. 5847 [UC]. **Los Angeles Co:** Pasadena, 27 Feb 1882, Jones, M. E. s.n. [CM]; San Clemente Island, 8 May 1962, Raven, P. H. 17609 [UC]. **Riverside Co:** 9.4 mi N of Blythe, 19 Feb 1958, Bacigalupi, R. 6188 [JEPS]; Marshall Canyon, 10 mi W of Coachella, 16 Apr 1905, Hall, H. M. 5797 [UC]; near Mecca, 28 Jun 1902, Parish, S. B. 8122 [UC]; S end of Coxcomb Mts, 27 Mar 1941, Wiggins, I. L. 966 [UC]. **San Bernardino Co:** NW side of Copper Basin, 6 May 1939, Alexander 710 [UC]; Sheep Hole Mts, 25 Apr 1932, Ferris, R. S. 8020 [UC]; Needles, 12 Mar 1919, Tidestrom, I. 8556 [UC]. **San Diego Co:** San Diego, 29 Apr 1902, Brandegee 832 [UC]; 6 mi NW of Agua Caliente, 5 Apr 1960, Everett 24075 [UC]; 1.5 mi E of Vallecitos, 28 Jan 1940, Munz, P. A. 15856 [UC]; Borrego Springs, 18 Mar 1976, Schroeder 51 [UC]. **San Luis Obispo Co:** San Luis Obispo, 9 May 1882, Jones, M. E. 3245 [UC]. **Santa Barbara Co:** Santa Ynez Mts, 9 May 1954, Pollard [UC].

Aristida californica Thurber in S. Watson, Bot. Calif. 2:289. 1880. Tufted, slightly bushy perennial; *culms* erect, much-branched, generally 10–40 cm tall; *internodes* glabrous or pubescent. *Sheaths* much shorter than the internodes, pubescent at the throat and on the collar. *Ligules* about 0.5 mm long. *Blades* mostly folded to involute, occasionally flat, stiffly spreading, 2–5 cm long, mostly less than 1 mm wide, scabrous to hispid-puberulent. *Inflorescence* few-flowered, 2–6 cm long, the terminal ones paniculate, the axillary ones racemose. *Glumes* unequal, 1-nerved. *Lemma* with a narrow column at the tip formed by the twisting and fusing of the awn bases; *awns* nearly equal, breaking from the lemma, the zone of articulation at the base of the awn column. $2n = 22$.

var. *californica*. CALIFORNIA THREEAWN (Fig. 2). *Internodes* pubescent, the hairs pilose to sublanose. *Glumes* very unequal, the first 4–8 mm long and the second 9–12 mm long. *Lemma* body 5–7 mm long when mature, the awn column 8–26 mm long; *awns* 2–4.5 cm long. Dry, sandy, desert areas. COUNTIES: Imperial, Riverside, San Bernardino, San Diego.

The other variety of this species is var. *glabrata* Vasey, known principally at the species level as *Aristida glabrata* (Vasey) Hitchcock. This variety differs from var. *californica* primarily in having glabrous, rather than pubescent, internodes and occur in the slightly higher elevations of the deserts to the east of the range of var. *californica*. Both taxa are diploids ($2n = 22$), and they overlap considerably in spikelet dimensions (Reeder and Felger 1989). Variety *glabrata* is not known from California.

SELECTED SPECIMENS.—**Imperial Co:** Signal Mt, 2 Apr 1903, Abrams, G. D. s.n. [DS-186664] [DS]; 8 mi E of El Centro, among larrea bushes, 22 Apr 1942, Beetle, A. A. 3172 [AHUC]; Bard, near Arizona line, 22 Sep 1912, Thornber, J. J. s.n. [ARIZ], a few mi E of Holtville, Jun 1951, Tofsrud, R. s.n. [AHUC]. **Riverside Co:** near Thousand Palms, rocky desert slopes, 27 Apr 1943, Beetle, A. A. 1938 [AHUC]; Pinto Basin, 16 mi from Cottonwood Springs, 15 May 1938, Ferris, R. S. 9522 [DS]; canyons along Colorado River, 1 May 1905, Hall, H. M. 5963 [ARIZ, POM, UC]; Coachella Valley, 6 mi SE of Garnet Station, sand dunes, ca 500 ft, 11 Mar 1928, Howell, J. T. 3443 [DS, CAS, AHUC]. **San Bernardino Co:** Joshua Tree National Monument, 1700 ft, north ledge, T1S R10E, 18 May 1941, Cole, J. E. 734 [UC]; Baxter, S of Mojave River, 23 May 1915, Parish, S. B. 9886 [UC, DS]; Dale Lake Valley (W of lake), 13 mi E of 29 Palms, sun-dry sand flats, abundant, 29 May 1941, Wolf, C. B. 10876 [RSA, DS, CAS]. **San Diego Co:** San Felipe Narrows, ca 350 ft, 20 Apr 1935, Jepson, W. L. 17101 [JEPS]; canyon W of Borrego Spring, 1500 ft, 19 Apr 1906, Jones, M. E. s.n. [POM-117001] [POM]; Colorado Desert, clay hills, 25 Jun 1888, Orcutt, C. R. 1486 [DS].

Aristida divaricata Humb. & Bonpl. ex Willdenow, Enum. Pl. 1:99. 1809. POVERTY THREEAWN (Fig. 3). Tufted perennials; *culms* erect, mostly unbranched, 25–70 cm tall; *internodes* glabrous. *Sheaths* longer than the internodes. *Ligules* 0.5–1 mm long. *Blades* loosely involute, glabrous, 5–20 cm long, 1–2 mm wide. *Panicle* open, 10–30 cm long, 6–25 cm wide; primary branches stiffly spreading from the main axis, axillary pulvini present, 2–12 cm long, generally naked on the lower portion. *Branchlets and spikelets* generally appressed along the branches, but sometimes spreading. *Glumes* nearly equal, 1-nerved, 8–12 mm long, acuminate-aristate. *Lemma* 8–13 mm long to base of awns, the terminal 2–3 mm narrowed and generally twisted four or more turns; *awns* subequal to unequal, (7)10–22 mm long, the lateral awns at least slightly shorter than the central. *Anthers* 0.8–1 mm long. $2n = 22$. To be looked for on dry slopes below 150 m elevation. COUNTIES: San Diego.

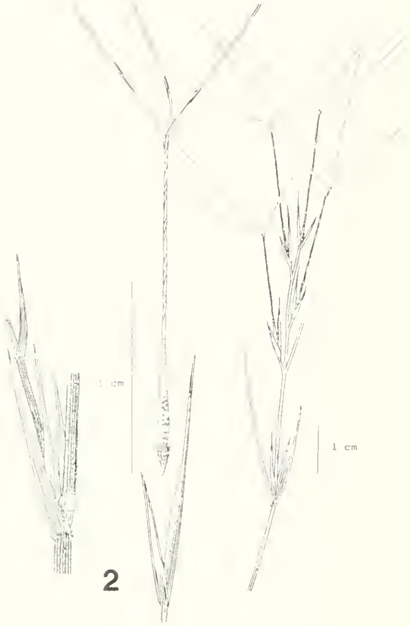

Fig. 2. *Aristida californica*, inflorescence, spikelet, and detail of branching.

It is doubtful that *Aristida divaricata* currently occurs in California. Most reports are based on collections of C. R. Orcutt in 1884, and no known specimens have been collected from the state since that time. In addition, it is possible that Orcutt's labels are in error, because on at least one specimen of *A. divaricata* he located Hansen's Ranch, which is in Baja California, in San Diego County.

A similar species, *Aristida orcuttiana* Vasey, also supposedly was collected from southern California in 1884 by C. R. Orcutt, and two specimens are housed at US. The labels describe San Diego as the collection locality, and these specimens are apparently the basis for reports of either *A. orcuttiana* or *A. schiedeana* Trinius & Ruprect from California (Abrams 1923, Jepson 1923, Hitchcock 1924, Munz & Keck 1968). Coincidentally, the type locality of *A. orcuttiana* is again Hansen's Ranch in Baja California, mentioned above. It is possible that neither *A. divaricata* nor *A. orcuttiana* was ever collected from California by Orcutt, but from

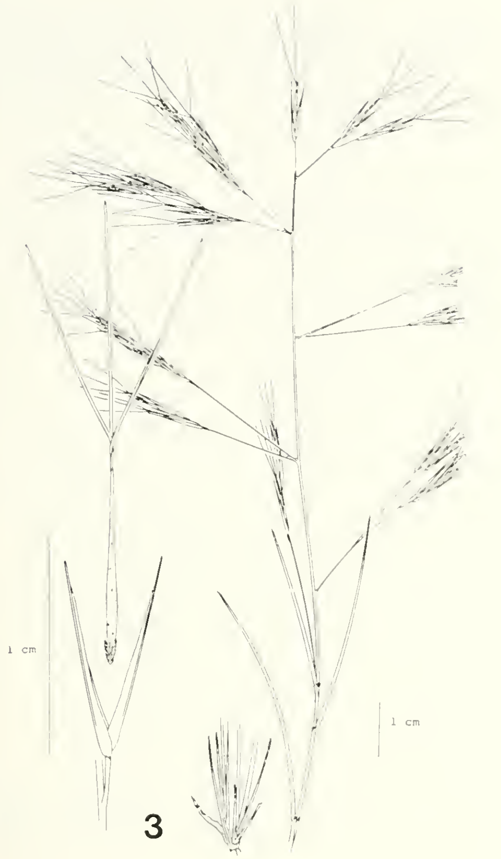

Fig. 3. *Aristida divaricata*, inflorescence, spikelet, and base of plant.

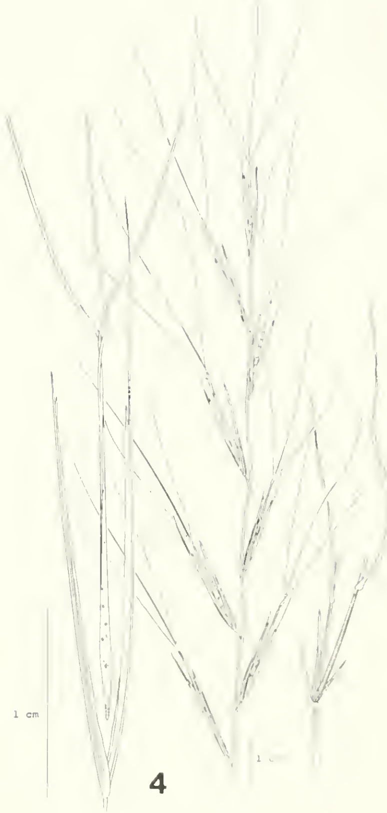

Fig. 4. *Aristida oligantha*, inflorescence, spikelet, and detail of branching.

Baja California. *Aristida orcuttiana* resembles *A. divaricata* in the stiffly spreading panicle branches, but the lateral awns are very short or absent, and the blades are generally flat and somewhat curling in *orcuttiana*.

SPECIMENS EXAMINED.—Without definite locality but recorded as California: Santa Catalina Mts [Santa Catalina Island?], in 1884, Orcutt, C. R. 2 [US]; Santa Clara Mountains [possibly Arizona?], in 1884, Orcutt, C. R. 2 [US]. **San Diego Co:** San Diego, Orcutt, C. R. s.n. [NY, US].

Aristida oligantha Michaux, Fl. Bor. Amer. 1:41. 1803. OLDFIELD THREEAWN (Fig. 4) [*A. oligantha* var. *nervata* Beal]. Tufted annuals; *culms* wiry, 30–70 cm tall, much-branched, the innovations extravaginal; *internodes* glabrous, pithy. *Sheaths* mostly shorter than the internodes. *Ligules* 0.1–0.5 mm long. *Blades* flat to involute, 3–22 cm long, 1–2 mm wide, reduced upwards. *Inflorescence* few-flowered, racemose, the spikelets nearly sessile. *Glumes* subequal or the second longer, awn-tipped, mostly (12)18–34 mm long, the first 3- to 5(7)-nerved and short-awned, the second 1- to 3-nerved with an awn 8–13 mm long. *Lemma* (10)13–20 mm long to base of awns; *central awn* (2)3.5–7 cm long, the *lateral awns* generally somewhat shorter. $2n = 22$. Dry hills and fields, bare ground, scrub land, 90–1000 m elevation. COUNTIES: Amador, Butte, El Dorado, Humboldt, Imperial, Lake, Madera, Mendocino, Merced, Modoc, Nevada, Placer, Redding, Sacramento, San Joaquin, Shasta, Siskiyou, Solano, Sonoma, Stanislaus, Tehama, Tuolumne, Yuba.

Some specimens of *Aristida oligantha* from northern California (Lake and Modoc counties) and adjacent areas of southern Oregon exhibit smaller glumes, lemmas, and awns than are typical and have been segregated as either *A. ramosissima* Engelmann var. *chaseana* Henrard or *A. oligantha* var. *nervata* Beal. In addition, the central awn in these plants in sometimes acutely reflexed and the florets darkened. This configuration is intermediate between *A. oligantha* and *A. ramosissima*.

SELECTED SPECIMENS: **Butte Co:** Chico, 27 Jul 1903, Copeland 3488 [US, WIS]; volcanic uplands between Pentz and Dry Creek, 15 Jul 1914, Heller, A. 11576 [UC]; 2.5 mi S of Wyandotte, 28 Nov 1933, Jensen 367 [UC]. **Humboldt Co:** Cottrell Ranch, 17 Sep 1955, Mallory 122 [UC]; Trinity River near mouth of Willow Creek, 15 Sep 1919, Tracy 5222 [UC]; vicinity of Garberville, 27 Aug 1933, Tracy 13000 [UC]; Dobbyn Creek, 9 Jul 1934, Tracy 13341 [UC]. **Lake Co:** dry hills between Upper Lake and Scott Valley, 17 Aug 1905, Tracy, J. P. 2365 [UC] (var. *nervata*). **Madera Co:** Minturn, 1 Oct 1936, Hoover, R. F. 1618 [JEPS, UC]. **Merced Co:** Tuttle, 17 Jul 1936, Hoover, R. F. 1580 [JEPS, UC]. **Modoc Co:** 19 Aug 1935, Whitney, L. 3627 [UC]; Fletcher Creek, 6 Sep 1935, Wheeler, L. C. 3959 [US] (var. *nervata*). **Nevada Co:** Tahoe Natl Forest, S of Grass Valley, Aug 1931, Smith 2638 [JEPS, UC]. **Sacramento Co:** 5 mi SE of Folsom, Yates, H. S. 5953 [UC]. **Shasta Co:** Redding, 21 Jun 1909, Blankinship [JEPS]; 1 mi N of Anderson, 21 Jul 1932, Long 190a [UC]. **Stanislaus Co:** vicinity of La Grange, 30 Sep 1961, Allen [JEPS]; between Knight's Ferry and Warnerville, 1 Sep 1941, Hoover, R. F. 5582 [UC]; 1 mi NW of Waterford, Yates, H. S. 6858 [UC]. **Tehama Co:** 9.7 mi N of Red Bluff, 14 Aug 1954, Baccigalupi, R. 4808 [JEPS]; Volcanic Plateau NE of Red Bluff, 22 Sep 1940, Hoover, R. F. 4617 [UC]. **Tuolumne Co:** near Keystone, Yates, H. S. 6148 [UC].

Aristida purpurea Nuttall, Trans. Amer. Philos. Soc. 5:145. 1837. Tufted perennials; *culms* erect and generally unbranched, 10–80 cm tall; *internodes* glabrous. *Sheaths* longer than the internodes. *Ligules* 0.1–0.5 mm long. *Blades* mostly involute. *Panicle* variable, contracted and spikelike to open and flexuous, the branches without pulvini in the axils (except var. *parishii*). *Glumes* mostly unequal (except var. *parishii*), the first about half the length of the second, 1(3)-nerved, acuminate. *Awns* about equal or the central slightly longer. Because of intergradation among forms (Allred 1984), the taxa of this complex are recognized as varieties within *Aristida purpurea*.

1. Primary panicle branches, at least the lower, with axillary pulvini and usually stiffly spreading to ascending from the main axis . . . . . . var. *parishii*

— Primary panicle branches lacking axillary pulvini, the spikelets variously disposed but at least the bases of the branches appressed to the axis 2

2(1). Awns 4–10 cm long 3

— Awns 1–3.5 cm long 4

3(2). Summit of lemma 0.1–0.3 mm wide; awns rather delicate, mostly 0.2 mm or less wide at the base, 4–6 cm long; second glume mostly shorter than 16 mm . . . . var. *purpurea*

— Summit of lemma 0.3–0.8 mm wide; awns usually stout, more than 0.2 mm wide at the base, 4–10 cm long; second glume 16–25 mm long . . var. *longiseta*

4(2). Summit of lemma mostly less than 0.2 mm wide; awns delicate, mostly less than 0.2 mm wide at the base 5

— Summit of lemma mostly more than 0.2 mm wide; awns stout, mostly 0.2 mm or more wide at the base 6

5(4). Panicle branches and pedicels erect, stiff, occasionally spreading or flexuous . . . . . var. *nealleyi*

— Panicle branches and pedicels drooping to flexuous . . . . var. *purpurea*

6(4). Panicles mostly 3–14 cm long; blades mostly basal and less than 10 cm long . . . . . . var. *fendleriana*

— Panicles mostly 15–30 cm long; blades mostly cauline and more than 10 cm long . . . var. *wrightii*

var. *fendleriana* (Steudel) Vasey, Contr. U.S. Natl. Herb. 3:46. 1892. FENDLER THREEAWN (Fig. 5) [*A. fendleriana* Steudel, Syn. Pl. Glum. 1:420. 1855]. *Culms* 10–40 cm tall. *Blades* involute, mostly less than 10 cm long, usually basal but occasionally cauline. *Panicle* 3–14 cm long, narrow. *Glumes* unequal, the first 5–8 mm long, the second 10–15 mm long. *Lemma* 8–14 mm long; *awns* generally 1.8–4 cm long, 0.2–0.3 mm wide at the base. $2n = 22, 44$. Dry, often rocky slopes and hills, 1000–2000 m elevation. COUNTIES: Inyo, Riverside, San Bernardino, San Diego.

SELECTED SPECIMENS.—**Inyo Co:** Devil's Kitchen Cyn, SE 1/4, Sec 7, T22S R39E, 21 May 1978, Zembal, R. L. 531 [RSA/POM]. **Riverside Co:** 20 Jul 1905, Griffiths, D. 8008 [MO]; San Jacinto Mts, Pinyon Flats, 18 May 1958, Raven, P. H. 13003 [RSA/POM]. **San Bernardino Co:** near Jupiter Mine, Kingston Range,

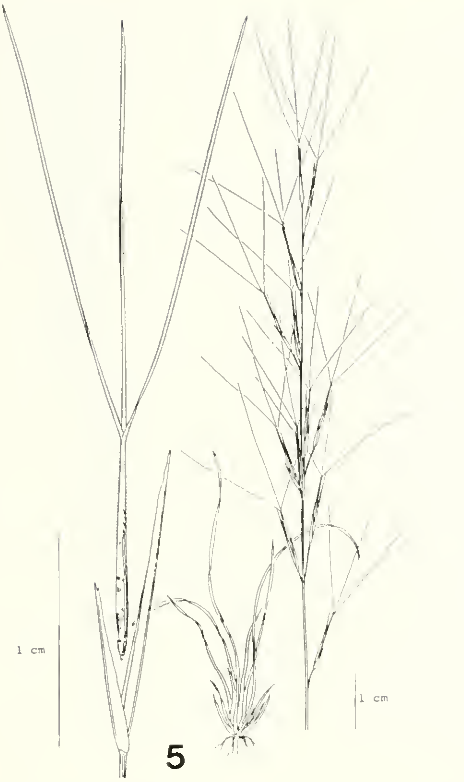

Fig. 5. *Aristida purpurea* var. *fendleriana*, inflorescence, spikelet, and base of plant.

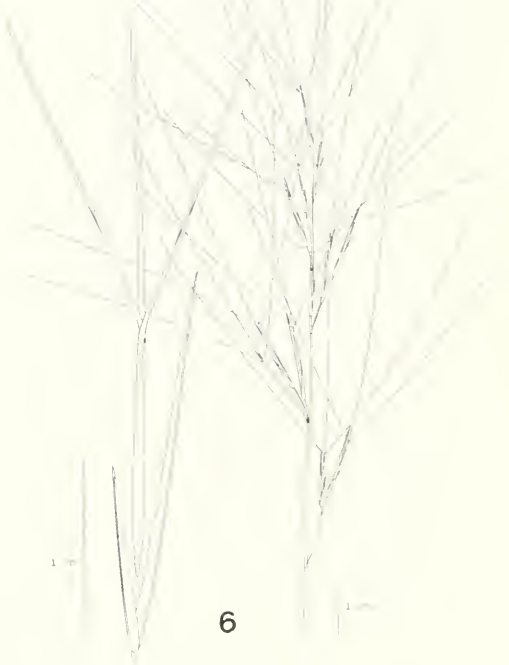

Fig. 6. *Aristida purpurea* var. *longiseta*, inflorescence and spikelet.

30 May 1980, de Nevers, G. 348 [RSA/POM]; SW New York Mts, 5.5 mi E of Cima in Cottonwood Canyon near Cottonwood Spring, 2 Jun 1973, Henrickson, J. 10339 [RSA/POM]; Ivanpah Mts, Kessler Peak, 2 Jun 1931, Jepson, W. L. 15825 [JEPS]; San Bernardino Mts, 15 Jun 1895, Parish, S. B. [UC]; Budweiser Wash, near 35d 46m N, 115d 44m W, Granite Mts, 28 Oct 1977, Prigge, B. A. et al. 2320 [RSA/POM]; Caruthers Cyn, New York Mts, 30 May 1973, Thorne, R. F. 43639 [RSA/POM]. **San Diego Co:** 3 mi WNW of Jacumba, Yates, H. S. 6805 [UC]; 5 mi ENE of Jacumba, Yates, H. S. 6808 [UC].

var. *longiseta* (Steudel) Vasey in Rothrock, U.S. Survey W. 100th Merid. Rpt. 6:286.1855. RED THREEAWN (Fig. 6) [*A. longiseta* Steudel, Syn. Pl. Glum. 1:420. 1855, *A. longiseta* var. *robusta* Merrill]. *Culms* 10–40 cm tall, delicate or stout. *Blades* 4–16 cm long, mostly involute, basal or cauline. *Panicle* 5–15 cm long, the branches stout and erect to delicate and drooping, but usually not very flexuous or tangled. *Glumes* unequal, the first 8–12 mm long, the second 16–25 mm long, sometimes shorter. *Lemma* 12–16 mm long, 0.4–0.8 mm wide just below the awns; *awns* stout, 4–10 cm long, 0.2–0.5 mm wide at the base. $2n$ = 22, 44, 66, 88. Dry, desert hills and plains, 300–1500 m elevation. COUNTIES: Mono, Riverside, San Bernardino, San Diego.

The varieties *longiseta* and *fendleriana* are often confused, but are most easily distinguished by the width of the awns and lemma apices, and not by whether the leaves are basal or cauline.

SELECTED SPECIMENS: **Riverside Co:** Joshua Tree National Monument, 1 May 1942, Roos 1153 [US]; Deep Canyon, T7S R5E, 27 Jun 1937, Yates, H. S. 6722 [RSA/POM]. **San Bernardino Co:** E New York Mts, W of Castle Buttes between Corral and Dove Spring, 12 May 1974, Henrickson, J. 13933 [RSA/POM]; Rock Springs, Palmer, E. 537 [UC]; plains near Leastalk, 3 Jun 1915, Parish, S. B. 10329 [UC]; 2.2 mi ESE of Brant on N side range of New York Mts, 8 May 1978, Prigge, B. A. et al. 2905 [RSA/POM]; San Bernardino Natl Forest, above Cactus Flat W of Hwy 18 N of Baldwin Lake, 2–3 Jun 1980, Thorne, R. F. 54375 [RSA/POM]. **San Diego Co:** head of Box Canyon near Mason Valley, 12 May 1932, Duran, V. 3208 [WIS].

var. *nealleyi* (Vasey in Coulter) Allred, Brittonia 36:391. 1984. NEALLEY THREEAWN (Fig. 7) [*A. glauca* (Nees) Walpers, *A. stricta* Michaux var. *nealleyi* Vasey in Coulter, Contr. U.S. Natl. Herb. 1:55. 1890]. *Culms* 20–45 cm tall, tightly clustered. *Blades* generally basal, involute, curving in age, 5–15 cm long. *Panicle* narrow, spikelike, light brown, 8–18 cm long, the branches mostly erect-appressed. *Glumes* mostly unequal, the first 4–7 mm long, the second 8–14 mm long. *Lemma* 7–13 mm long, 0.1–0.2 mm wide just below the awns; *awns* delicate, 1.5–2.5 cm long, mostly 0.1 mm wide at the base. $2n = 22, 44$. Dry, desert plains and slopes, 200–1200 m elevation. COUNTIES: Imperial, Inyo, Riverside, San Bernardino, San Diego.

Variety *nealleyi* grades into var. *purpurea* with flexuous branches, and into var. *wrightii* with more robust panicles and broader lemma apices and awns.

SELECTED SPECIMENS.—**Imperial Co:** Painted Gorge, Carisso Mts, 17 May 1938, Ferris, R. S. 9623 [UC]. **Inyo Co:** Johnson Creek, Death Valley, 28 Apr 1940, Gilman, M. F. 4190 [RSA/POM]; Cave Springs Wash, 25 Apr 1930, Hoffman, R. [US]; Funeral Mts, 2 May 1917, Jepson, W. L. 6907 [JEPS]; Titanothere Cyn, Grapevine Mts, E side of Death Valley, 26 Mar 1947, Wiggins, I. L. 11566 [RSA/POM, UC]. **Riverside Co:** Cottonwood Spring, 30 Mar 1940, Hitchcock, C. L. 5871 [MO, RSA/POM, UC]; Eagle Mts, Cottonwood Springs, 25 Apr 1928, Jepson, W. L. 12585 [JEPS]; mouth of Andreas Canyon, 4–6 April 1917, Johnston, I. M. 1010 [RSA/POM]; E of Hemet, along San Jacinto River, 7 Aug 1938, Roos, J. C. 582 [RSA/POM]. **San Bernardino Co:** Providence Mts, Fountain Canyon, 15 May 1937, Beal 301 [JEPS]; route 95, 18 mi N of Travis, 23 Apr 1942, Beetle, A. A. 3193 [WIS]; 39 mi from Needles on Parker Road, 24 Apr 1928, Ferris, R. S. 7226 [RSA/POM]. **San Diego Co:** San Felipe, 16 Apr 1895, Brandegee [UC]; San Felipe Gap, 6 Apr 1901, Brandegee [UC]; head of Fox Canyon near Mason Valley, 12 May 1932, Duran, V. 3208 [MICH, MO, RSA/POM, UC]; Yaqui Well, 22 Apr 1928, Jepson W. L. 12516 [JEPS].

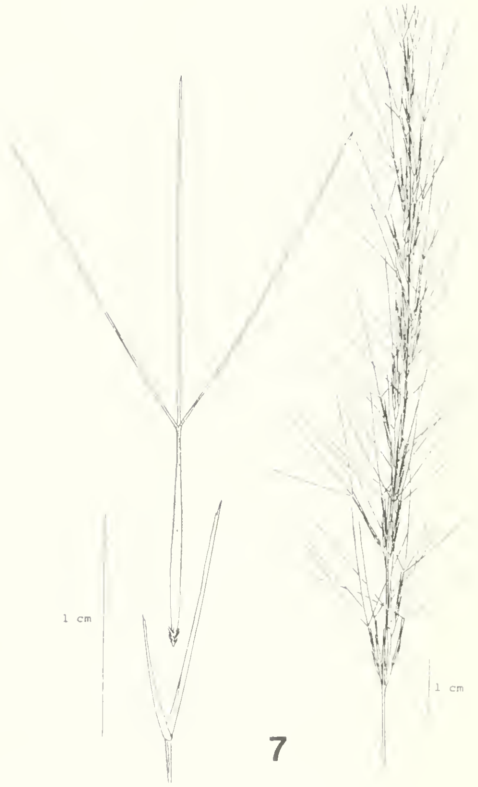

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Fig. 7. *Aristida purpurea* var. *nealleyi*, inflorescence and spikelet.

var. *parishii* (A. S. Hitchcock in Jepson) Allred, Brittonia 36:392. 1984. PARISH'S THREEAWN (Fig. 8) [*A. parishii* A. S. Hitchcock in Jepson, Fl. Calif. 1:101. 1912, *A. wrightii* Nash var. *parishii* (Hitchcock in Jepson) Gould]. *Culms* thick, stout, erect. *Blades* mostly flat, longer than 10 cm. *Panicle* narrow, spikelike or the lower branches with axillary pulvini and spreading at about a 45-degree angle, 15–24 cm long, reddish when young. *Glumes* unequal to equal, the first 7–11 mm long, the second 10–15 mm long. *Lemma* 10–13 mm long, 0.2–0.3 mm wide just below the awns; *awns* 2–3 cm long, 0.2–0.3 mm wide at the base. Chromosome number not reported. Dry hills and plains, 300–1000 m elevation. COUNTIES: Imperial, Inyo, Los Angeles, Riverside, San Bernardino, San Diego.

Variety *parishii* is very similar to var. *wrightii* but differs most strikingly in the sometimes spreading primary branches, the reddish color of the panicle when young, and the more clustered arrangement of the spikelets. It also

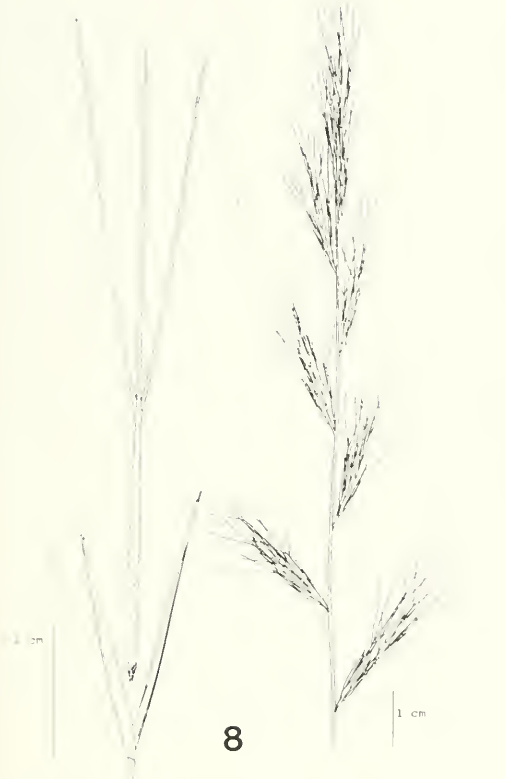

Fig. 8. *Aristida purpurea* var. *parishii*, inflorescence and spikelet.

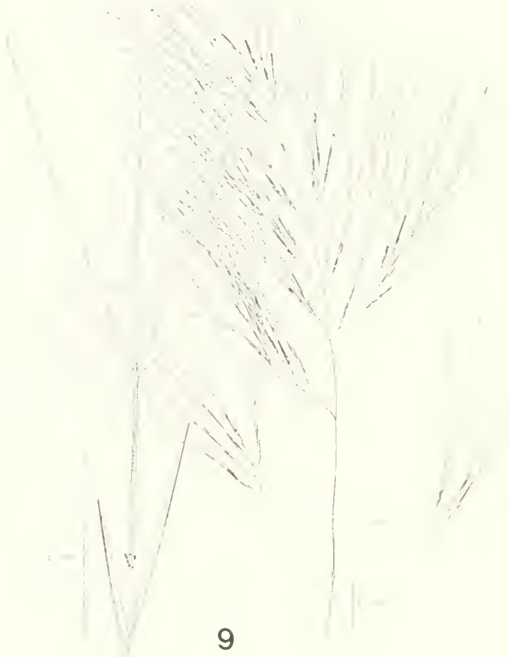

Fig. 9. *Aristida purpurea* var. *purpurea* inflorescence and spikelet.

flowers earlier, mostly March through May, while var. *wrightii* flowers mostly May through October. Parish's threeawn also resembles some members of the Divaricatae group because of its spreading primary branches and generally subequal glumes.

SELECTED SPECIMENS.—**Imperial Co:** 9.2 miles NE of Glamis, 18 Mar 1962, Hitchcock, C. L. 2225 [F]; Palo Verde Mts, 8 Apr 1949, Roos, J. C. 4198 [US]. **Inyo Co:** specimen without locality at RSA/POM. **Riverside Co:** Chuckawalla Springs, 15 mi SE of Guiladay, 9 Jul 1957, Crampton, B. s.n. [AHUC]; Palm Canyon, 4 Apr 1917, Johnston, I. M. 1008 [US, MICH]; Riverside and vicinity of upper fork of Salt Creek Wash, 19 Mar 1927, Reed, F. M. 5440 [AHUC, RSA/POM]; between March AFB and Lakeview, 29 Apr 1966, Roos, J. C. s.n. [RSA/POM]. **San Bernardino Co:** 2 mi NE of Fifteenmile Point, 3000 ft, 28 Apr 1935, Axelrod, D. 321 [AHUC, UC]; between Bullion and Sheep Hole Mts, 7 Apr 1940, Munz, P. A. 16568 [RSA/POM]; Budweiser Wash, near 35d 46m N, 115d 44m W, Granite Mts, 28 Oct 1977, Prigge, B. A. et al. 2320 [RSA/POM]. **San Diego Co:** 0.5 mi N of Miramar Reservoir, clay soil, 4 Mar 1981, Reveal, J. s.n. [AHUC]; Anza Canyon E of Julian, 3 Apr 1940, Wilson, E. s.n. [AHUC].

var. *purpurea*. PURPLE THREEAWN (Fig. 9) [*A. purpurea* var. *californica* Vasey]. *Culms* 25–60 cm tall. *Blades* flat to involute, mostly cauline, 3–17 cm long, 1–2 mm wide. *Panicle* purplish, often nodding, 10–25 cm long, the branches usually delicate, drooping or flexuous. *Glumes* unequal, the first 4–9 mm long, the second 7–16 mm long. *Lemma* 6–12 mm, 0.1–0.3 mm wide just below the awns; *awns* 2–3(4) cm long, 0.2–0.3 mm wide at the base. $2n = 22$, 44, 66, 88. Dry, grassy hills, scrub lands, 250–800 m elevation. COUNTIES: Mono, Riverside, San Bernardino, San Diego.

This is a beautiful grass, with its drooping, reddish, plumelike panicles. It commonly intergrades with the varietes *nealleyi*, *longiseta*, and *wrightii*.

SELECTED SPECIMENS. **Mono Co:** McAfee Creek, White Mts, Fishlake Valley drainage, 6 Aug 1984, Morefield, J. D. JDM-2480 e [RSA/POM]. **Riverside Co:** 1 mile E of Banning,

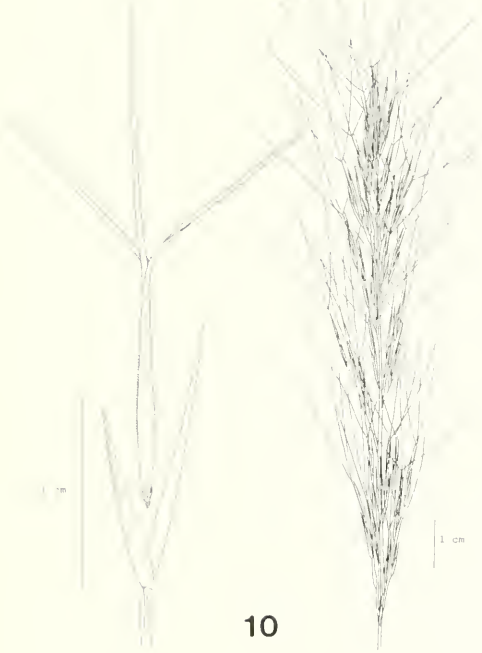

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Fig. 10. *Aristida purpurea* var. *wrightii*, inflorescence and spikelet.

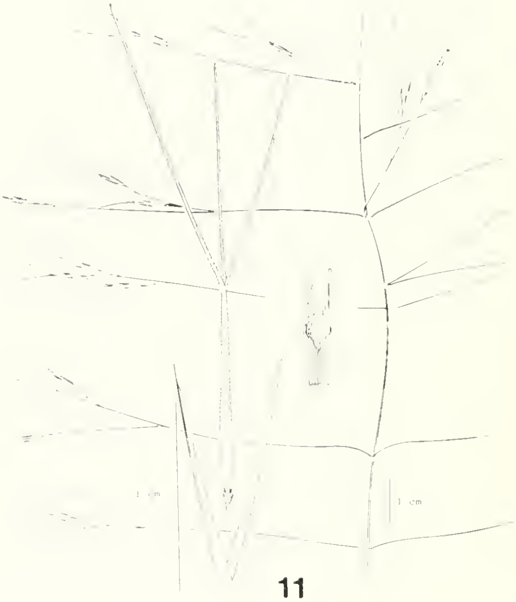

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Fig. 11. *Aristida ternipes* var. *hamulosa*, inflorescence, spikelet, and detail of ligular region.

20 Jul 1905, Griffiths, D. 8007 [MO]; Palm Canyon, 4 Apr 1917, Johnston, I. M. 1008 [US, MICH]; base of San Jacinto Mountain, June 1882, Parish, S. B. et al. 1549 [F, MICH]; Lower San Jacinto River Canyon, Yates, H. S. 6711 [UC]. **San Bernardino Co:** road from Highland to Running Springs, 1 mi from valley floor, 26 Jun 1942, Beetle, B. A. 3644 [F, WIS]; near Upland, 7 Nov 1916, Johnston, I. M. 1120 [MICH]; San Bernardino Valley, 2 Jun 1906, Parish, S. B. 5783 [NMCR]; Clark Mts, 5 Aug 1950, Roos, J. C. et al. 4906 [RSA/POM, UC]. **San Diego Co:** 6 mi N of Ocean Side Ranch, coast hills in chaparral, 21 Apr 1942, Beetle, A. A. 3145 [TAES]; near Vallecitos Station, 2 Apr 1939, Gander, F. 7142 [MICH]; Harbison Canyon, 19 Jun 1938, Gander, F. F. 5999 [RSA/POM].

var. *wrightii* (Nash in Small) Allred, Brittonia 36:393. 1984. WRIGHT'S THREEAWN (Fig. 10) [A. *wrightii* Nash in Small, Fl. Southeast. U.S. 116. 1903]. *Culms* erect, to 80 cm tall. *Blades* involute to flat, cauline, 10–25 cm long, 1–3 mm wide. *Panicle* narrow, spikelike, 14–30 cm long, the branches erect-appressed. *Glumes* unequal, the first 5–10 mm long, the second 10–16 mm long. *Lemma* 8–14 mm long, 0.2–0.3 mm wide just below the awns; *awns* mostly 2–3.5 cm long, 0.2–0.3 mm wide at the base. $2n = 22, 44, 66$. Sandy or rocky hills and plains, 500–1500 m elevation. COUNTIES: Riverside, San Bernardino, San Diego.

Wright's threeawn intergrades with the varieties *purpurea*, *fendleriana*, and *parishii*.

SELECTED SPECIMENS.—**San Bernardino Co:** Slover Mts, 14 Aug 1907, Reed F. M. 1307 [WIS]; 2.5 mi SE of Kingston Peak, T19N R10E, Sec 34-27, 23 Oct 1977, Henrickson, J. 16321 [RSA/POM]; rocky canyon between Bullion and Sheep Holt Mts, 7 Apr 1940, Munz, P. A. 16568 [UC]. **San Diego Co:** 3 mi WNW of Jacumba, T18S R8E, 3 Sep 1937, Yates, H. S. 6805 [RSA/POM].

Aristida ternipes Cavanilles, Icon. Pl. 5:46. 1799. Tufted perennials; *culms* few, erect to sprawling, simple or only weakly branched, 25–80 cm tall; *internodes* glabrous. *Sheaths* mostly longer than the internodes. *Ligules* 0.2–0.5 mm long. *Blades* flat to involute, 5–40 cm long, 1–2 mm wide, with scattered long hairs above the ligule. *Panicle* 15–40 cm long, open, the branches widely spreading from the main axis and naked at the base, axillary pulvini present.

Spikelets appressed or spreading from the branches. *Glumes* about equal, 1-nerved, 9–15 mm long. *Lemma* 10–15 mm long, usually not twisted at the apex; *awns* equal to very unequal. *Anthers* 1.2–3 mm long.

var. *hamulosa* (Henrard) Trent, Sida 14(2):260. 1990. HOOK THREEAWN (Fig. 11) [*A. hamulosa* Henrard, Med. Rijks Herb. Leiden 54:219. 1926]. *Central awn* 10–25 mm long. *Lateral awns* mostly 6–23 mm long, sometimes shorter. $2n = 44$. Dry hills and slopes, 100–800 m elevation. COUNTIES: Butte, Colusa, Fresno, Glenn, Kern, Los Angeles, Madera, Riverside, San Bernardino, San Diego, Santa Barbara, Sonoma, Stanislaus, Sutter, Tehama, Tulare, Ventura, Yolo.

Trent and Allred (1990) documented the morphologic variation and similarity of *Aristida ternipes* and *A. hamulosa*, concluding that the *hamulosa* taxon should be treated as a variety of *ternipes*. Variety *ternipes* does not occur in California and differs only in the length of the lateral awns. Variety *hamulosa* also resembles *A. divaricata*, which differs most consistently in having shorter anthers and lacking pilose hairs above the ligule. Based on numbers of specimens in California herbaria, var. *hamulosa* is unusually common.

SELECTED SPECIMENS.—**Butte Co:** South Butte, 10 Sep 1981, Ahart 1535 [UC]; along Hwy 32, 1 mi E of Chico, 16 Aug 1983, Ahart, L. 4277 [TAES]. **Colusa Co:** 10 mi W of Williams, 5 Jul 1955, Burcham, L. T. 317 [AHUC, TAES, UC]; 10.7 mi SE of Leesville, 19 May 1958, Crampton, B. 4789 [AHUC]. **Fresno Co:** Citrus Grove, 11 May 1940, Hoover, R. F. 4385 [UC]; 8 mi N of Orange Cove, 8 Jun 1960, Howell, J. T. 35481 [ISC]. **Glenn Co:** 5.5 mi S of Orland, 29 May 1942, Beetle, A. A. et al. 3353 [AHUC]; 5 mi W of Orland on the Newville road, 27 May 1914, Heller, A. A. 11432 [US]. **Kern Co:** lowest slopes of the Tehachapi Mts, 15 mi S of Bakersfield, 14 Apr 1942, Beetle, A. A. 3017 [AHUC]; 15 mi S of Bakersfield, 7 Jun 1946, Beetle, A. A. 4679 [UC]. **Los Angeles Co:** Alta Dena, 2 Apr 1905, Grant 66-6459 [ARIZ, RSA/POM, UC]; Pomona, 1 Jul 1937, Horton 448 [UC]; Liveoak Canyon, San Gabriel Mts, 15 Apr 1934, Wheeler, L. C. 2525 [AHUC]. **Madera Co:** near Raymond, on sheep ranch, 11 May 1934, Wilson, E. s.n. [AHUC]. **Riverside Co:** 10 mi N of Pala, 17 Mar 1964, Hitchcock, C. L. et al. 23113 [NY]; lower San Jacinto River Canyon, Yates, H. S. 6710 [UC]. **San Bernardino Co:** near Upland, 7 Nov 1916, Johnston, I. 1121 [ARIZ]; mesa near Rialto, 20 May 1888, Parish, S. B. [UC]; Granite Mountains, Budweiser Wash, 28 Oct 1977, Prigge, B. A. et al. 2321 [RSA/POM]. **San Diego Co:** Rolando, 14 Jan 1938, Gander, F. F. 4936 [SD]; San Jamento, 4 Jul 1890, Hasse, H. E. s.n. [NY]; Escondido, 10 Aug 1928, Meyer 652 [JEPS]. **Santa Barbara Co:** Santa Cruz island, N of biological station in central valley, 23 Apr 1979, Thorne, R. F. et al. 52466 [RSA/POM]. **Sonoma Co:** Little Geysers, 1 mi E of Big Sulphur Creek, 10 Aug 1984, Leitner [UC]. **Stanislaus Co:** vicinity of La Grange, 30 Sep 1961, Allen, P. s.n. [AHUC, JEPS]. **Sutter Co:** Sutter Buttes, 10 Sep 1981, Ahart L. 3129 [NY]. **Tehama Co:** about 5 km N of Black Butte Reservoir and about 17 km NW of Orland, 26 Mar 1990, Buck, R. 1469 [JEPS]; Jelly's Ferry Rd, 0.5 mi from I-5 exit, 16 Aug 1991, Allred, K. W. 5467 [NMCR]. **Tulare Co:** Three Rivers, 24 Aug 1905, Brandegee s.n. [UC]; 10 mi SE of Porterville on Tule Indian Reservation Rd, 28 Dec 1964, Guthrie, L. 66 [AHUC]; Fountain Springs Rd, 6.3 mi W of California Hot Springs, 25 Jun 1966, Twisselmann, E. C. 12537 [AHUC]. **Ventura Co:** Upper Santa Ana Creek, Santa Ynez foothills, 13 Jun 1957, Pollard, H. M. s.n. [TAES]. **Yolo Co:** foothills, open slope, 2 mi W of Winters, 24 Aug 1953, Crampton, B. 1600 [AHUC].

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TEMPERATURE-MEDIATED CHANGES IN SEED DORMANCY AND LIGHT REQUIREMENT FOR *PENSTEMON PALMERI* (SCROPHULARIACEAE)

Stanley G. Kitchen[1] and Susan E. Meyer[1]

Abstract.—*Penstemon palmeri* is a short-lived perennial herb colonizing disturbed sites in semiarid habitats in the western USA. In this study seed was harvested from six native and four seeded populations during two consecutive years. In laboratory germination trials at constant 15 C, considerable between-lot variation in primary dormancy and light requirement was observed. Four weeks of moist chilling (1 C) induced secondary dormancy at 15 C. Cold-induced secondary dormancy was reversed by one week of dark incubation at 30 C. This warm incubation treatment also reduced the light requirement of unchilled, after-ripened seed. Fluctuations in dormancy and light requirement of buried seeds have been linked to seasonal changes in soil temperature. *Penstemon palmeri* germination responses to temperature appear to be similar to those of facultative winter annuals.

Key words: seed germination, Palmer penstemon, seed bank, induced dormancy, beardtongue, Penstemon palmeri.

Seed dormancy mechanisms function to ensure that germination is postponed until conditions are favorable for seedling survival (Fenner 1985). The level of dormancy of an imbibed seed is dependent upon its dormancy level prior to imbibition and on the environmental conditions to which it has been exposed in the imbibed state (Bewley and Black 1982).

Chilling, essential for breaking dormancy in seeds of many temperate species, induces varying degrees of secondary dormancy in others (Baskin and Baskin 1985). Conversely, warm temperatures increase and diminish dormancy in other species. These temperature-mediated changes in seed dormancy are related to the season in which seeds undergo germination and emergence. Thus, spring and fall germinators tend to have opposite responses to chilling and warm-temperatures regimes.

Penstemon palmeri Gray is a short-lived perennial herb native to the southern half of the Great Basin and adjoining regions of the western United States (Cronquist et al. 1984). It occurs across a fairly broad range in elevation (800–2750 m), colonizing relatively open, early successional sites such as roadcuts and washes. Individual plants produce large quantities of seed that remain viable for several years in storage (Stevens et al. 1981). Numerous populations have been successfully established through artificial seeding on a variety of sites outside its native range (Stevens and Monsen 1988). This versatility raises questions about the establishment strategy of this species. In this study the effects of moist chilling and warm incubation on seed germinability were determined under controlled laboratory conditions. The results are sufficiently clear to permit speculation about seedbed ecology and have led to the fieldwork necessary to confirm the conclusions drawn herein.

In laboratory trials on *P. palmeri*, Young and Evans (unpublished data, Great Basin Experimental Range, Ephraim, Utah) demonstrated that germination at a constant 15 C was not significantly lower than at any other constant or alternating temperature regime. Germination over a 28-day period was suppressed at mean temperatures below 10 and above 25 C. Allen and Meyer (1990) reported similar results in a study of three *Penstemon* species and suggested the possibility of cold-induced secondary dormancy in *P. palmeri*. Field sowing of this species is usually carried out in late fall and is based on the assumption that a cold treatment is required to break dormancy (Stevens and Monsen 1988).

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METHODS

Seed Acquisition

Ripened seeds were harvested from nine populations in 1986. Collections were made from eight of the original and one new population in 1987 (Table 1). Four of the populations were from roadside seedings outside the native range of this species. The genetic origin of the artificially seeded populations is unknown. Each collection was cleaned using standard techniques and stored in envelopes at 20 C (room temperature).

Viability Determination

An estimate of viability for each 1986 collection was obtained using a tetrazolium chloride (TZ) test. Four replications of 25 seeds from each collection were imbibed overnight. Each seed was pierced and placed in a 1% TZ solution at room temperature for 24 hours. Embryos were then evaluated for viability using established procedures (Grabe 1970).

Gibberellic acid (GA$_3$) effectively breaks dormancy in *P. palmeri* seeds (Young and Evans, unpublished data, Great Basin Experimental Range, Ephraim, Utah). Four replications of 25 seeds for each 1986 collection were imbibed in 250 mg L^{-1} GA$_3$. Germination temperature was a constant 15 C. Germination percentages, determined after 21 days, showed no significant differences between TZ estimates of viability and germination percentages in GA$_3$. Hence, germination in GA$_3$ was the only measure of viability employed with 1987 seed.

Experiment I

Experiment I was started on 1 June 1987. Mean time after harvest date was approximately nine months (Table 1). The experiment was designed to determine the effect of three temperature pretreatments on germination of seed from the nine 1986 collections under two light regimes. Pretreatments included: (1) chilling for 28 days at 1 C, (2) incubation for 7 days at 30 C, (3) chilling for 28 days at 1 C followed by incubation for 7 days at 30 C, and (4) no pretreatment. Germination temperature and duration following pretreatment was a constant 15 C for 21 days. The light regimes were a 12-hr photoperiod and constant darkness.

Each pretreatment/light regime combination was replicated four times for each of the nine collections. Replicates consisted of 25 seeds placed on top of two germination blotters in a 100 × 15-mm petri dish. Blotters were moistened to saturation with deionized water.

Experimental units assigned the same pretreatment and light regime were randomized in stacks of 10. A blank dish (blotters but no seeds) was placed on top of each stack that would receive light, ensuring that all seeds would receive light through the sides of the dish only. Light intensity inside the dishes was 25 microeinsteins m^{-2} sec^{-1} PAR. Each stack was enclosed in a plastic bag and loosely sealed with a rubber band to retain moisture and facilitate handling.

During pretreatment, stacks were placed in cardboard boxes, each of which was enclosed in an additional plastic bag. After pretreatment, stacks assigned the light regime were removed from their boxes and randomly arranged in the growth chamber directly beneath fluorescent lights. The remaining boxes were placed in the growth chamber and were not opened until the end of their germination period.

Seeds with radicle extension >1 mm were counted as germinated. Experience with this and other penstemon species has shown this to be a clear indicator of the initiation of seedling development. A germination percentage was determined for each replicate (dish). Germination percentages were arcsine transformed for statistical analysis. Experimental results were subjected to analysis of variance procedures appropriate to the completely randomized design. Because of the collection × treatment interaction in the analysis of variance, each collection and treatment was analyzed independently. Significant differences among treatment and collection means were determined using the Student-Neuman-Keul (SNK) method.

Experiment II

A second experiment was started on 14 October 1987 using nine fresh (1987) collections (Table 1). Mean time from harvest was approximately one month. The objective was to determine the effect of 30 C (imbibed) on primary dormancy and light requirement of fresh seed. The methods were the same as those used in the first experiment with three exceptions: only one pretreatment was used (30 C), the length of the pretreatment was 14 days, and the length of germination was 28 days. Light and dark controls (no warm incubation) were again included.

TABLE 1. Location and harvest dates for 10 populations (18 collections during two years) of *P. palmeri*. All populations are in Utah except the Mountain Home population in Idaho.

				Harvest date	
Collection	Lat (N)	Long (W)	Elevation (m)	1986	1987
Snow's Canyon	37°12′	113°39′	1080		8/14
Browse	37°21′	113°15′	1350	8/22	8/14
Leeds	37°14′	113°21′	1050	8/8	8/14
Zion	37°14′	112°54′	1740	8/22	9/14
Kolob Road	37°16′	113°06′	1440	8/8	9/13
Utah Hill	37°08′	113°47′	1380	8/8	
Mountain Home[a]	42°57′	115°05′	930	8/13	8/27
Mercur Canyon[a]	40°25′	112°10′	1650	12/15	9/22
Salt Creek Canyon[a]	39°42′	111°45′	1740	9/10	10/10
Nebo Loop[a]	39°52′	111°40′	2100	10/26	10/10

[a] Artificially seeded populations from outside the natural range

RESULTS

Experiment I

Four weeks of chilling reduced germination in light significantly below the level of controls for six of the nine collections (Table 2). Incubation at 30 C caused no significant change for germination in light when compared to the control. When the four-week chill was followed by one week at 30 C, mean germination percentage was only slightly lower than that of the control. This indicates that incubation at 30 C effectively reversed the secondary dormancy induced by chilling. In addition, incubation at 30 C substantially increased the dark germination percentage over the dark control (Table 3). The 30 C warm incubation was much less effective in removing the light requirement when preceded by chilling.

Germination rate at 15 C was only slightly accelerated by chilling and warm incubation pretreatments (data not shown). Mean germination for the light control treatment after seven days was 15%, indicating that most essentially nondormant seeds required a considerable period of imbibition before germination was possible. Four weeks of chilling and one week of warm incubation increased the proportion of seeds that germinated by day 7 to 24 and 28%, respectively. However, a major fraction of the seeds still required more than one week of constant imbibition at 15 C to germinate.

Experiment II

In the first experiment there was a slight trend in the more dormant lots for germination to be higher after warm incubation relative to the control. The second experiment was conducted to determine if warm incubation could break the primary dormancy of fresh seeds.

Contrary to what was expected for fresh seed, only two of the nine 1987 collections showed significant primary dormancy (Table 4). The increase in germination percentage following warm incubation was significant when compared to the nonincubated light control for one of these collections. In the remaining collections, neither the light control nor the light, warm-incubated germination percentages were significantly different from total viability estimates determined by germination in GA_3.

The variation in dark germination was similar to that observed in the first experiment with after-ripened seed (Table 4). The effect of warm incubation on dark germination was not as clear as in the initial experiment. Germination of the warm-incubated seeds resulted in a mean net increase over nonincubated, dark controls of only 11%. Four of the nine collections showed significant increases, while one showed a decrease.

DISCUSSION

Moist chilling for four weeks caused varying degrees of secondary dormancy in *P. palmeri* seed collections. Incubation at 30 C clearly

TABLE 2. Germination response of nine after-ripened collections of *P. palmeri* seed to moist chilling (1 C for 28 days) and warm incubation (30 C for 7 days). The germination period was for 21 days at a constant 15 C with a 12-hr photoperiod. Germination in 250 mg L^{-1} GA_3 was used as an estimate of total viability for each collection.

	Mean germination percentage[a]				
		Pretreatment			
Collection	Control	1 C	30 C	1 C/30 C	GA_3
Browse	90a	41b	92a	86a	91a
Leeds	89a	38c	92a	73b	93a
Zion	72a	73a	80a	71a	81a
Kolob Road	95a	63b	90a	86a	97a
Utah Hill	89a	39b	88a	78a	82a
Mountain Home	88ab	65b	89ab	87ab	92a
Mercur Canyon	86b	21c	87b	81b	99a
Salt Creek Canyon	58b	55b	80ab	72b	92a
Nebo Loop	75a	38b	84a	80a	89a
Means	82b	48d	87b	79c	91a

[a]Within a collection, means followed by the same letter are not significantly different at the $p < .05$ level (SNK).

broke cold-induced secondary dormancy in after-ripened seed, and there is some indication that it can reduce levels of primary dormancy as well. The warm-induced reduction in light requirement was less pronounced for fresh compared to after-ripened collections.

The response of *P. palmeri* seeds to moist chilling and warm incubation parallels those observed for fall germinators (winter annuals) (Baskin and Baskin 1985). This is supported by the lack of primary dormancy in freshly harvested seeds. Nevertheless, a significant portion of the seeds was not induced into secondary dormancy during chilling. This suggests that late winter/early spring germination of some seeds is likely. It is of little surprise that recently emerged seedlings were found in *P. palmeri* populations in both spring and fall. Such bimodal germination patterns are typical of facultative winter annuals (Baskin and Baskin 1985) and would be selected for in unpredictable habitats where the best season for seedling survival may differ from year to year (Silvertown 1984). Such germination patterns would also be adaptive for species that colonize different kinds of habitats with varying degrees of threat from frost and drought. Both situations occur within the range of *P. palmeri*.

Given its small seed size (Plummer et al. 1968), a light requirement for germination of *P. palmeri* is not surprising (Fenner 1985). The level of active phytochrome in dry seeds and, subsequently, light sensitivity is strongly influenced by conditions during ripening (Cresswell and Grime 1981, Gutterman 1982) and may vary considerably among the seeds of a single plant (Silvertown 1984). The *P. palmeri* seeds in these experiments demonstrated three levels of response to light, suggesting variable levels of total or active phytochrome in the seeds. Some seeds germinated in the dark while others required light, and a few remained dormant even with light. The proportion of seeds that could germinate in the dark was increased by incubation at 30 C (Table 3).

Light sensitivity can be altered by temperature shifts during seed imbibition (Toole 1973, Franklin and Taylorson 1983). This may be due to temperature effects on the production, destruction, or dark reversion of phytochrome. Temperature shifts may also alter other factors associated with phytochrome action, thus resulting in an increase or decrease in light sensitivity. Hendricks and Taylorson (1978) suggested that temperature effects on phytochrome action in seeds may be due to changes in membrane fluidity. It is likely that the effects of temperature on light sensitivity in seeds are a result of more than one process acting in concert.

A light requirement may help determine season of germination for buried *P. palmeri* seeds. Habitats with adequate winter snows provide enough moisture for spring germination of surface seed. Long periods (8–16 weeks) of

TABLE 3. The effect of chilling (1 C for 28 days), warm incubation (30 C for 7 days), and chilling followed by warm incubation on the light requirement of nine after-ripened collections of P. palmeri. The germination temperature was 15 C.

	Germination percentage[a]				
	Light	Dark			
Collection	Control	Control	1 C	30 C	1 C:30 C
Browse	90a	56c	32d	75b	17e
Leeds	89a	45c	16d	68b	13d
Zions	72a	37c	35c	55b	24c
Kolob Road	95a	49c	31c	77b	34c
Utah Hill	89a	41b	23b	70a	33b
Mountain Home	88a	54b	59b	87a	65ab
Mercur Canyon	86a	42b	6c	83a	38b
Salt Creek Canyon	58a	26b	34b	76a	46ab
Nebo Loop	75a	12c	8c	61a	35b
Means	82a	40c	27e	72b	34d

[a]Within a collection, means followed by the same letter are not significantly different at the $p < .05$ level (SNK).

TABLE 4. Primary dormancy, light requirement, and the effect of warm incubation (14 days at 30 C) on the germination of nine fresh collections of P. palmeri seed. The germination period was 28 days at 15 C. Light treatments received a 12-hr photoperiod. Germination in GA_3 (250 mg L^{-1}) was used as a measure of viability for each collection.

	Germination percentage[a]				
	Control		30 C pretreatment		
Collection	Light	Dark	Light	Dark	GA_3
Snow's Canyon	94a	31b	85a	34b	97a
Browse	86a	25c	80a	53b	93a
Leeds	92a	35b	91a	51b	92a
Zions	70a	38b	72a	24c	74a
Kolob Road	83a	30b	88a	17b	87a
Mountain Home	96a	56b	87a	66b	94a
Mercur Canyon	87a	58b	87a	76a	94a
Salt Creek Canyon	77bc	45d	86b	67c	98a
Nebo Loop	55b	16c	74a	40b	81a
Means	82b	37d	83b	48c	90a

[a]Within a collection, means followed by the same letter are not significantly different at the $p < .05$ level (SNK).

moist chilling reduce the time needed for germination to occur, thus increasing the chances of spring-germination and seedling establishment from seeds not induced into secondary dormancy (Kitchen and Meyer, unpublished data on file at the Shrub Sciences Laboratory, Provo, Utah). Rapid drying of the soil surface would make the germination of surface seeds following summer or autumn rains less likely. Buried seeds with a light requirement are functionally dormant and would contribute to the seed bank. Apparently, chilling does not reduce the light requirement in *P. palmeri* seeds, while warm incubation eliminates it in a significant fraction of the seeds (Table 3). This suggests that buried seeds may be more likely to germinate in the fall after experiencing sufficient warm incubation to eliminate their light requirement.

Whether current-year *P. palmeri* seeds germinate in the fall or spring may depend as much on time of seed dispersal as temperature and moisture conditions that follow. The collection dates for each population (Table 1) and field observations regarding the timing of fruit dehiscence suggest that populations from areas with milder winters (lower elevations) tend to ripen and disperse seed during late summer. At higher elevations where cold weather would occur earlier, seed ripening and dispersal are delayed.

Habitats with mild winters and unpredictable spring moisture seem to favor early dispersal and fall germination. Such sites select for the maintenance of a seed bank because extended periods of drought are typical and conditions for successful establishment may not be met for many years. Cold-induced secondary dormancy and burial of light-requiring seeds should facilitate the buildup of this soil seed reserve. In habitats with more severe winter conditions dispersal is retarded and spring germination of a portion of the seeds is both probable and less risky. The preservation of a seed reserve through cold-induced dormancy may also be important in these more mesic habitats.

Penstemon palmeri appears to be adapted for establishment in a variety of habitats. Two phenomena are important in this success. First, individual seeds seem to be capable of responding appropriately to different environmental stimuli. Second, variability in germination response among seeds within a population is indicative of a bet-hedging strategy increasing the chances for successful establishment across a range of variabe and unpredictable environments. Habitat-related between-population variation in germination timing mechanisms appears to be relatively unimportant.

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LATE QUATERNARY ARTHROPODS FROM THE COLORADO PLATEAU, ARIZONA AND UTAH

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ABSTRACT—Late Quaternary-age arthropods were recovered from dry cave deposits and packrat middens located in the Grand Canyon, Canyonlands, and Glen Canyon region of the Colorado Plateau. This Quaternary data resource has not been analyzed before from the Colorado Plateau national parks. Radiocarbon dates on the various deposits containing arthropods range from 1510 to 30,660 yr B.P. The fossil assemblages yielded 57 identified taxa of insects, arachnids, and millipedes, including 15 taxa taken to the species level. The information from the fossil insect record of the Colorado Plateau is not yet sufficiently detailed to permit precise paleoenvironmental reconstructions. However, preliminary conclusions suggest a cooler, moister climatic regime during the late Wisconsin glacial and a mosaic of vegetation types, such as grassland and shrubby communities, unlike the present vegetation at the localities.

Key words: Quaternary, Colorado Plateau, arthropods, Wisconsin glacial, Grand Canyon, caves.

This paper discusses the results of a preliminary study of late Quaternary arthropod fossils from cave deposits and packrat middens from southern Utah and northern Arizona. This Quaternary data source has not been analyzed before from the Colorado Plateau, although the arid Southwest has been the focus of paleoenvironmental studies for approximately half a century (Antevs 1939). Arid climate, coupled with episodic fluctuating water tables, has proven detrimental to the preservation of most exposed fossil remains. However, the same xeric conditions, when coupled with a stable rock shelter, provide a unique situation—dry preservation. Such xeric locations provide the preservation of not only pollen and plant macrofossils, but also soft tissues and other usually degradable remains of animals (such as skin, hair, keratinous tissues, and dung; Wilson 1942). The study of packrat middens in the Southwest has provided a reconstruction of the Wisconsin glacial biological communities never before observable in such detail (see various chapters in Betancourt et al. 1990). Thus, an entirely new field of research has been opened, and it should prove valuable in understanding the latest Pleistocene.

Dry cave deposits were quickly discovered to be a warehouse of late Pleistocene information. Gypsum Cave (near Las Vegas, Nevada) and Rampart Cave (western Grand Canyon, Arizona) were the scenes of the first paleoecological studies utilizing dry-preserved dung of an extinct animal. Laudermilk and Munz (1934, 1938) found a wealth of information preserved in the dung of extinct Shasta ground sloth (*Nothrotheriops shastensis*). Later studies concerned with dietary reconstructions expounded on the data available from dung of extinct herbivores, including Shasta ground sloth, mammoth (*Mammuthus*), Harrington's mountain goat (*Oreamnos harringtoni*), and bison (*Bison*), among others (Martin et al. 1961, Hansen 1980, Davis et al. 1984, Mead, O'Rourke, and Foppe 1986, Mead, Agenbroad et al. 1986, Mead et al. 1987, Mead and Agenbroad 1989).

Packrats (*Neotoma;* Rodentia; Cricetidae) build nests surrounded by construction materials collected from within 30 to 100 m of the house. The construction components are predominantly plant materials, but the packrat also collects small stones, skeletal remains, and dung. Adding to the materials procured by the packrat are various vertebrates and invertebrates who live in the nest and waste pile as commensals. Periodic house cleaning produces a waste pile of debris. Urination on the waste pile (a midden) ultimately may cement the remains into a rock-hard deposit, encapsulating

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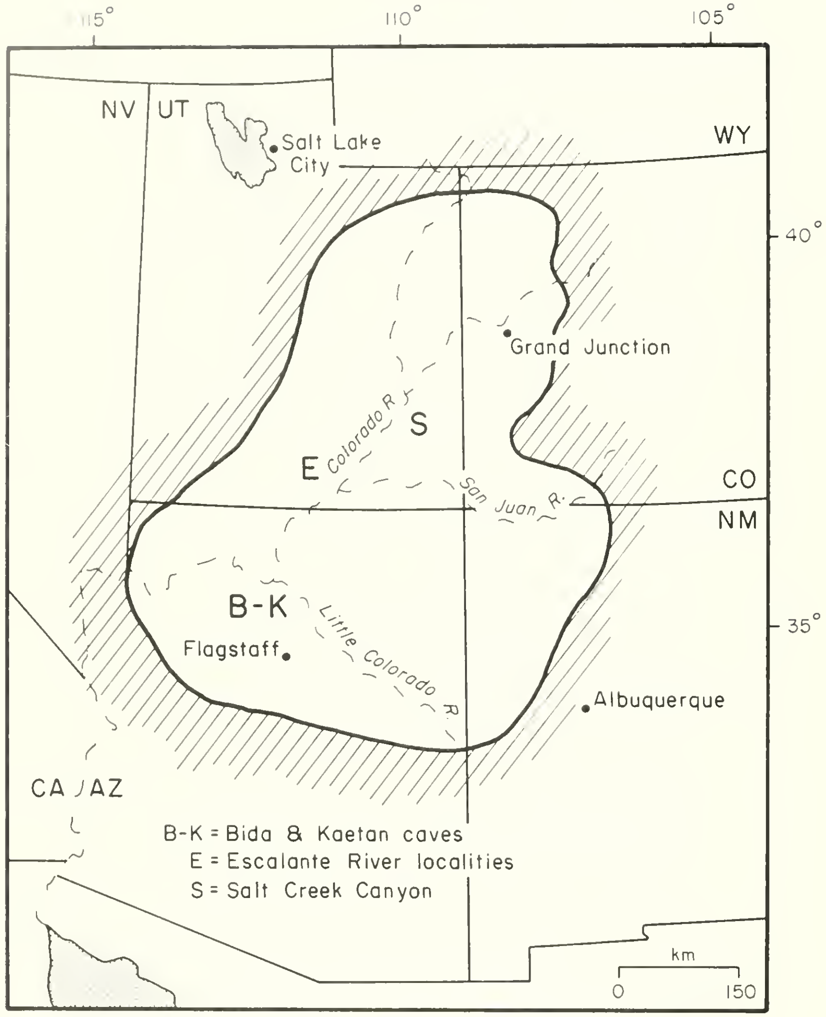
115°
110°
105°
40°
35°
NV
UT
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NM
CA
AZ
Salt Lake City
Grand Junction
Flagstaff
Albuquerque
Colorado R.
San Juan R.
Little Colorado R.
S
E
B-K
B-K = Bida & Kaetan caves
E = Escalante River localities
S = Salt Creek Canyon
km
0
150

Fig. 1. Map of the Colorado Plateau with sites discussed in text.

the contents of that time. When these indurated (cemented) middens are located in a dry alcove, rock shelter, or cave, the contents may be preserved for as long as the shelter exists. Radiocarbon dating of indurated midden layers provides a chronological framework for the associated plant and animal remains. Middens, then, provide a unique examination of local past biotic communities.

The investigation of insect fossils from ancient packrat middens and cave deposits is a new approach that is just beginning to show substantial results. One of the authors (SAE) recently performed more extensive research on a series of insect fossil assemblages from packrat middens in the Chihuahuan desert regions of western Texas and south central New Mexico (Elias 1987, Elias and Van Devender 1990, 1991). Elias (1990) also recently published the results of a taphonomic study designed to reveal the sources and possible biases of insect exoskeletons in packrat middens.

METHODS

Localities

Matrices from packrat middens and cave sediments were washed or hand picked for arthropod and other animal and plant remains. Packrat midden and cave deposits from two cave sites were analyzed from Grand Canyon National Park (GRCA), Coconino County, Arizona; three packrat middens from Salt Creek, Canyonlands National Park (CANY), San Juan

County, Utah; and three packrat middens and one cave deposit from the Escalante River region of Glen Canyon National Recreation Area (GLCA), Kane County, Utah (Fig. 1).

Bida Cave is a large limestone cave located in pinyon-juniper woodland at 1430 m elevation in GRCA. Cole (1990) reported on the packrat middens recovered from the cave. Test pit excavations produced a multitude of faunal and floral remains (Mead 1983, O'Rourke and Mead 1985, Mead, O'Rourke, and Foppe 1986, McVickar and Mead ms). Radiocarbon dates (spanning from 2960 to 24,190 yr B.P.) on various remains are presented in Mead (1983) and Mead, Martin et al. (1986); those ages from units containing arthropod remains are listed in Table 1.

Kaetan Cave is a medium-sized limestone cave at 1430 m elevation in GRCA. Mead (1983) excavated portions of the deposit in the entrance room for the remains of extinct mountain goat (*Oreamnos harringtoni*) (O'Rourke and Mead 1985, Mead, O'Rourke, and Foppe 1986). Paleoenvironmental reconstruction based on the macrobotanical remains recovered from packrat middens and stratified sediments is in manuscript (McVickar and Mead). Radiocarbon ages span the period from 14,220 to 30,600 yr B.P. (Table 1).

Three packrat middens selected from a series collected from Salt Creek Canyon, CANY (1505 to 1755 m elevation), have radiocarbon ages spanning 3830 to 27,660 yr B.P.; today the region is pinyon-juniper woodland with sagebrush flats. The analysis of the macrobotanical remains and paleoenvironmental reconstructions of the middens is in manuscript (Mead and Agenbroad).

Bechan Cave contains copious remains of extinct herbivore dung (Davis et al. 1985, Mead, Agenbroad et al. 1986, Mead and Agenbroad 1989) recovered from floor sediments dating 11,600 to 13,505 yr B.P. Arthropods were recovered from the dung layer and from an isolated Holocene-age packrat midden in the cave (Table 1). Other nearby packrat middens contained additional arthropod remains dating from 1510 to 8640 yr B.P.

Insects

Fossil insect sclerities were sorted from washed packrat middens and cave sediment matrices. Robust specimens were mounted on modified micropaleontological cards with gum tragacanth, a water-soluble glue. Fragile specimens and duplicates were stored in vials of alcohol. Fossils were identified chiefly through comparisons with modern identified specimens in the U.S. National Museum of Natural History (Smithsonian Institution), Washington, D.C. Some specimens were referred to taxonomic specialists, as noted in the acknowledgments. Modern ecological requirements and distributions for species identified in the fossil assemblages were compiled from the literature and from specimen labels in the U.S. National Museum. All specimens will be curated in the National Park Service Repository, Laboratory of Quaternary Paleontology, Quaternary Studies Program, Northern Arizona University.

TABLE 1. Late Quaternary deposits and radiocarbon dates from sites on the Colorado Plateau containing arthropods.

Locality	^{14}C age	Lab number
Grand Canyon National Park, Arizona		
Bida Cave		
Layer 2	2960 ± 200	A-2836
Layer 4	16,150 ± 600	RL-1135
Layer 5	none	—
Layer 8	24,190 + 4300 − 2800	A-2373
Kaetan Cave		
Layer 1	14,220 ± 320	A-2835
Layer 3	17,500 ± 300	A-2723
Layer 5	none	—
Layer 6	30,600 ± 1800	A-2722
Layer 8+	none	—
Packrat midden 1b	17,100 ± 500	A-2719
Owl Roost		
R2	21,430 ± 1500	A-3082
2	none	—
Canyonlands National Park, Utah		
Salt Creek Canyon (packrat middens)		
Dead Owl 1A	3830 ± 70	Beta-18267
Woodenshoe 1	6980 ± 120	Beta-27214
Hoodoo 1	27,660 ± 340	Beta-27213
Glen Canyon National Recreation Area, Utah		
Escalante River region (packrat middens)		
Bechan Cave 3	1510 ± 60	Beta-23706
Cow-Perfect 1	1820 ± 100	Beta-23711
Bowns 1	8640 ± 140	Beta-23704
Bechan Cave 158	11,600–13,505	[*]

[*] A series of dates are analyzed on *Mammuthus* (mammoth) and cf. *Euceratherium* (shrub ox) dung (see Davis et al. 1985, Mead, Agenbroad et al. 1986, Mead and Agenbroad ms).

Results

The fossil assemblages yielded 57 identified taxa of insects, arachnids, and millipedes, including 15 taxa taken to the species level. Table 2 shows the taxa identified from the

TABLE 2. Fossil arthropods identified from Bida and Kaetan caves, GRCA, Arizona, in minimum number of individuals per sample.

Taxon	Bida Cave				Kaetan Cave					
	2[a]	4	5	8	1[b]	5	8	ORR2[c]	OR2[d]	1b[e]
Coleoptera										
Carabidae										
Calosoma cf. *scrutator* Fab.	1	—	—	—	—	—	—	—	—	—
Agonum (*Rhadine*) *perlevis* Csy.	2	—	—	—	—	—	—	—	—	—
Agonum (*Rhadine*) sp.	—	1	1	—	—	—	—	—	—	—
Scarabaeidae										
Aphodius nr. *ruficlarus* Fall	—	—	—	1	—	—	—	—	—	—
Aphodius sp.	—	—	—	1	—	—	—	—	—	—
Onthophagus sp.	—	—	—	1	—	—	—	—	—	—
Serica sp.	1	—	—	—	—	1	—	2	1	—
Phyllophaga sp.	—	—	1	—	—	—	—	1	—	—
Diplotaxis sp.	1	—	—	—	—	—	—	1	—	—
Genus indeterminate	1	—	—	—	—	1	—	1	—	—
Silphidae										
Thanatophilus truncatus Say	1	—	—	—	—	—	—	—	—	—
Ptinidae										
Ptinis ap.	—	—	—	—	—	—	—	1	—	—
Niptus cf. *ventriculus* LeC.	—	—	—	—	10	1	—	9	—	4
Nitidulidae										
Genus indeterminate	—	—	—	—	—	1	—	—	—	—
Dermestidae										
Genus indeterminate	—	—	1	—	1	—	—	1	—	—
Histeridae										
Genus indeterminate	—	1	—	—	—	—	—	—	—	—
Elateridae										
Genus indeterminate	—	—	—	—	1	—	—	—	—	—
Tenebrionidae										
Eleodes cf. *nigrina* LeC.	—	—	—	—	1	—	—	4	—	—
Eleodes spp.	1	1	1	—	1	4	2	4	1	1
Coniontis sp.	—	—	—	—	—	1	—	—	—	—
Meloidae										
Genus indeterminate	—	—	—	1	—	—	—	—	—	—
Melandryidae										
Anaspis rufa Say	—	—	—	1	—	—	—	—	—	—
Chrysomelidae										
Lema trilinea White	—	—	—	—	—	1	—	—	—	—
Chaetocnema sp.	1	—	—	—	—	—	—	—	—	—
Genus indeterminate	—	—	—	—	1	—	—	—	—	—
Cleridae										
Acanthoscelides sp.	—	—	—	—	—	—	—	1	—	—
Curculionidae										
Sapotes sp.	—	—	1	—	—	—	—	—	—	—
Ophryastes sp.	—	2	—	1	—	—	—	—	—	—
Scyphophorus acupunctatus Gyll.	2	1	1	—	—	—	—	—	—	—
Orimodema protracta Horn	1	—	—	—	—	—	—	—	—	—
Cleonidius trivittatus or *C. quadrilineatus*	—	1	1	—	—	—	—	—	—	—
Apleurus angularis (LeC.)	—	1	—	—	—	—	—	—	—	—
Genus indeterminate	—	1	1	1	—	—	—	—	—	—
Scolytidae										
Genus indeterminate	—	—	—	1	—	—	—	—	—	—
Neuroptera										
Myrmeleontidae										
Genus indeterminate	—	—	—	—	1	—	—	—	—	—
Homoptera										
Cicadidae										
Genus indeterminate	—	—	—	—	1	—	—	—	—	—
Hemiptera										
Genus indeterminate	—	—	—	—	—	—	—	—	1	—

TABLE 2 CONTINUED.

Taxon	Bida Cave 2[a]	4	5	8	Kaetan Cave 1[b]	5	8	ORR2[c]	OR2[d]	1b[e]
ORTHOPTERA										
ACRIDIDAE										
Genus indeterminate	—	1	—	—	—	—	—	—	—	—
LEPIDOPTERA										
Genus indeterminate	—	—	—	1	—	—	—	—	—	—
HYMENOPTERA										
APOIDEA										
Genus indeterminate	—	—	—	—	1	—	—	—	—	—
DIPTERA										
Genus indeterminate	2	—	2	—	—	—	—	—	—	8
ARACHNIDA										
ACARI										
IXODIDAE										
Dermacentor andersoni Stiles	—	2	—	—	1	—	—	—	—	—
Dermacentor sp.	—	—	—	—	—	—	—	—	1	—
SCORPIONIDA										
BUTHIDAE										
Centuroides sp.	—	—	—	1	—	—	—	—	—	—
DIPLOPODA										
Genus indeterminate	—	1	1	—	—	—	—	—	—	—

[a] Numbers refer to layer numbers at Bida Cave.
[b] Numbers refer to layer numbers at Kaetan Cave
[c] Owl Roost R2
[d] Owl Roost 2.
[e] Packrat midden 1b.

Grand Canyon region, and Table 3 lists taxa identified from Glen Canyon. The assemblages are dominated by taxa still found today in the American Southwest, but many of the Pleistocene assemblages contain species that live today at elevations higher than the fossil localities. As in other packrat midden and cave assemblages from the American Southwest, the fossil faunas are dominated by a few families of insects and arachnids. The beetle (Coleoptera) families Carabidae (ground beetles), Curculionidae (weevils), Ptinidae (spider beetles), Scarabaeidae (dung beetles and chafers), and Tenebrionidae (darkling beetles) were represented in most assemblages. A few packrat and other mammalian parasites were found, including a tick (Ixodidae) and a blood-sucking bug (Reduviidae) that are known to parasitize packrats in their nests. A number of the identified species merit individual discussion.

Discussion of Selected Species

The ground beetles from the fossil assemblages include both cave dwellers and open-ground species. The caterpillar hunter, *Calosoma scrutator*, was found in a late Holocene assemblage from the Grand Canyon (Table 2). This beetle is widespread in the United States, southern Canada, and northern Mexico (Gidaspow 1959). It has been collected from the floor of Havasu Canyon, GRCA (Elias, unpublished data). The cave beetle, *Agonum perlevis* (Fig. 2A), preys on other arthropods. It is relatively common in caves and near the mouths of mammal burrows. It is found today from the state of Chihuahua, Mexico, northwest to southern Arizona (Barr 1982). This species, found in late Holocene assemblages in both the GLCA and GRCA regions, was identified from Holocene packrat middens from sites in the Chihuahuan desert region of Mexico (Elias and Van Devender, unpublished data). Another ground beetle from the late Holocene record at GLCA is *Discoderus impotens*, which lives in open country. It is common throughout the American Southwest and is found in the Chihuahuan, Sonoran, and Mojave deserts.

The checkered beetle (Cleridae), *Cymatodera pallida* (Fig. 2E), is a predator of bark beetles in coniferous forests in the Chiricahua, Rincon, and Huachuca mountains of Arizona, as well as in mountainous regions of Chihuahua, Mexico (Vaurie 1952). *C. pallida* was found in a late Pleistocene sample from the Grand Canyon.

The dung beetle (Scarabaeidae), *Aphodius ruficlarus*, was found in a late Pleistocene

TABLE 3. Fossil arthropods identified from the Canyonlands and Glen Canyon region, Utah, in minimum number of individuals per sample.

	CANY[a]			GLCA[b]			
Taxon	DO1A[c]	WS1	HD1	BC3[d]	C-P1	B1	BC15S
COLEOPTERA							
CARABIDAE							
Agonum (Rhadine) perlevis Csy.	—	—	—	2	—	—	—
Amara sp.	—	1	—	—	—	—	—
Discoderus impotens LeC.	—	—	—	1	—	—	—
Genus et sp. indeterminate	—	1	—	1	—	—	—
SCARABAEIDAE							
Aphodius spp.	—	—	—	—	—	—	2
Ataenius sp.	—	—	—	—	—	—	2
Serica sp.	—	—	—	1	—	—	—
Melolontha sp.	—	—	—	—	—	—	1
Diplotaxis sp.	—	—	—	1	—	—	—
Genus et sp. indeterminate	—	1	—	—	—	—	—
PTINIDAE							
Niptus sp.	10	—	1	1	—	2	—
Ptinus spp.	—	—	—	1	—	—	—
ELATERIDAE							
Genus et sp. indeterminate	—	2	—	—	1	—	—
BYRRHIDAE							
Genus et sp. indeterminate	—	—	—	—	1	—	—
TENEBRIONIDAE							
Eleodes spp.	—	—	1	1	—	—	—
Coniontis sp.	—	—	—	1	—	—	—
Genus et sp. indeterminate	1	—	—	—	—	—	—
DERMESTIDAE							
Genus et sp. indeterminate	1	—	—	—	—	—	—
CHRYSOMELIDAE							
Altica sp.	—	—	—	—	—	1	—
Pachybrachis sp.	—	1	—	—	—	—	—
Genus et sp. indeterminate	—	1	—	—	—	—	—
CLERIDAE							
Cymatodera pallida Schffr.	—	—	—	—	—	—	1
HOMOPTERA							
REDUVIIDAE							
Triatoma sp.	—	—	—	1	—	—	—
LEPIDOPTERA							
Genus et sp. indeterminate	—	—	1	—	—	—	—
HYMENOPTERA							
FORMICIDAE							
Formica sp.	1	—	—	—	—	—	—

[a] CANY = Canyonlands National Park

[b] GLCA = Glen Canyon National Recreation Area

[c] Sites in Canyonlands are: DO1A, Dead Owl 1A; WS1, Woodenshoe 1; HD1, Hoodoo 1

[d] Sites in Glen Canyon are: BC3, Bechan Cave 3; C-P1, Cow Perfect 1; B1, Bowns 1; BC15S, Bechan Cave 15S

assemblage from GLCA. This beetle lives today throughout much of western North America from Saskatchewan in the north to New Mexico, Arizona, and California in the south. At the southern limit of its range, it lives in mountainous regions.

The carrion beetle (Silphidae), *Thanatophilus truncatus* (Fig. 2B), lives in the southwestern U.S. and northern Mexico in habitats spanning altitudinal gradients from grasslands and arid scrub desert through oak-pinyon-juniper woodlands, pine forests, and montane meadows (Peck and Kaulbars 1987). *T. truncatus* was found only in a late Holocene assemblage from the Grand Canyon.

The spider beetle (Ptinidae), *Niptus ventriculus*, is a scavenger that ranges from Texas westward to California and south through Mexico to Guatemala. It probably breeds in rodent nests. Modern specimens have been collected from packrat nests and from the fur of kangaroo rats, *Dipodomys* spp. (Brown 1939, Papp 1962). This beetle species was common in several assemblages from GLCA.

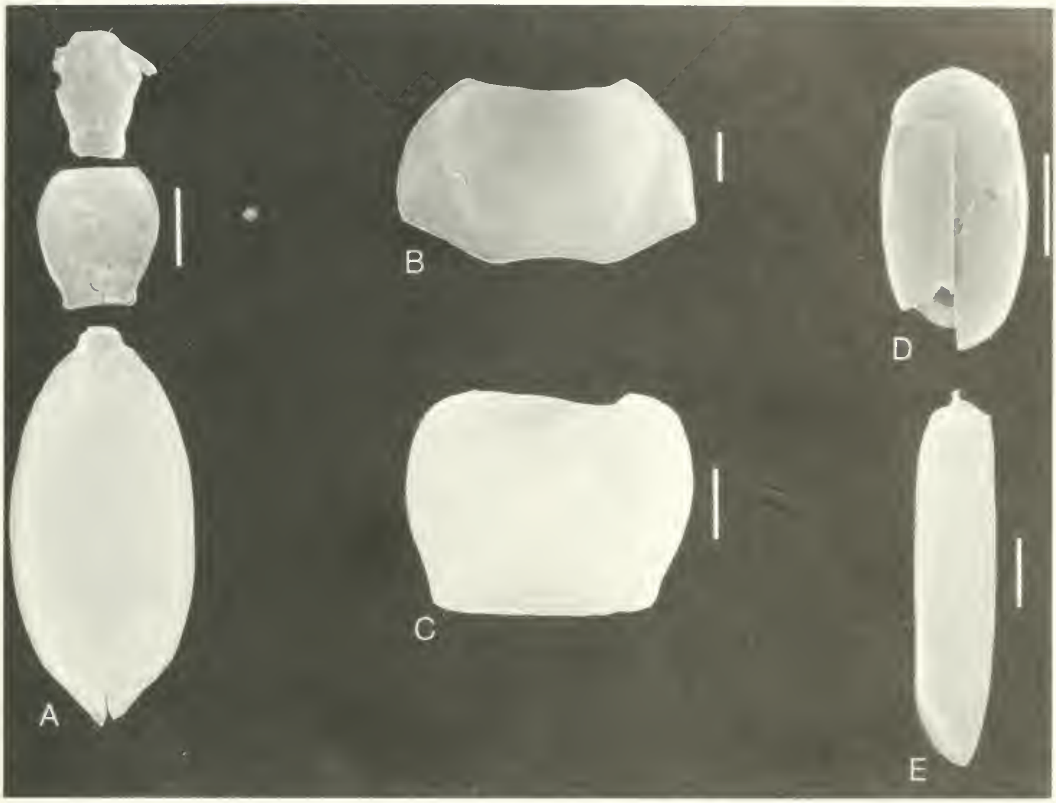

Fig. 2. Scanning electron micrographs of fossil beetles from sites discussed in text: A, head capsule, pronotum, and elytra of *Agonum perlevis* from the Bowns packrat midden, Glen Canyon; B, pronotum of *Thanatophilus truncatus* from Bida Cave, Grand Canyon; C, pronotum of *Eleodes nigrina* from Kaetan Cave, Grand Canyon; D, exoskeleton of *Anaspis rufa* from Bida Cave, Grand Canyon; E, left elytron of *Cymatodera pallida* from Hoodoo packrat midden, Canyonlands. Scale bar equals 1 mm.

The darkling beetle (Tenebrionidae), *Eleodes nigrina* (Fig. 2C), was found in a late Pleistocene assemblage from the GLCA. This scavenger is known today from the Pacific Northwest south to the mountains of Arizona. It is a cold-hardy species, found at elevations up to 3050 m in the Colorado Rockies (Blaisdell 1909).

The false darkling beetle (Melandryidae), *Anaspis rufa* (Fig. 2D), is widespread today. Beetles in this family are found under bark, in fungi, and in decaying logs (Liljeblad 1945).

The leaf beetle (Chrysomelidae), *Lema trilinea*, feeds on *Datura* (jimson weed) and other plants in the southern half of the United States. It was identified from a late Pleistocene assemblage in the GRCA. Other plant-feeding beetles identified from the fossil assemblages include the weevils (Curculionidae) *Scyphophorus acupunctatus*, *Orimodema protracta*, *Apleurus angularis*, and *Cleonidius trivattatus* or *C. quadrilineatus*, all from the Grand Canyon assemblage. Of these, *O. protracta* was found only in the late Holocene, *A. angularis* and *C. trivittatus* or *C. quadrilineatus* were found only in the late Pleistocene, and *S. acupunctatus* was identified from both periods. *O. protracta* lives at elevations from 2250 to 2700 m in the mountains of Arizona. It is a soil dweller that feeds on roots (R. S. Anderson, National Museum of Natural Sciences, Ottawa, written communication, July 1990). *A. angularis*, *C. trivittatus*, and *C. quadrilineatus* are all widespread today throughout western North America, while *S. acupunctatus* has been collected from Arizona and Mexico, where it feeds on *Agave*, *Dasylirion* (sotol), and *Lophophora* (peyote) (R. S. Anderson, National Museum of Natural Sciences, Ottawa, written communication, July 1990).

Finally, the tick (Ixodidae), *Dermacentor andersoni*, is found today in the western United States as far east as Montana. Immature

D. andersoni parasitize small mammals, while the adult stage parasitizes large mammals. This tick is a vector for Rocky Mountain spotted fever and Colorado tick fever (J. Keirans, National Institutes of Health, Bethesda, Maryland, written communication, June 1990).

PALEOENVIRONMENTAL INTERPRETATIONS

The information from the fossil insect record of the Colorado Plateau region is not yet sufficiently detailed to allow precise paleoenvironmental reconstructions. However, for both the Grand Canyon and Glen Canyon regions, the available insect data suggest a cooler, moister climatic regime during the late Pleistocene. Montane-adapted species lived at lower elevations. The insects document the presence of conifers at the sites but also suggest that a mosaic of vegetation types was locally represented, including grassland and shrubby terrain. The shift to postglacial climates occurred sometime after 14,000 yr B.P., and the most arid conditions appear to have developed within the last 1500 years. Additional studies of regional insect assemblages will undoubtedly clarify the nature and timing of environmental changes.

Although preliminary and incomplete in nature, the arthropod data presented here are in agreement with the detailed plant reconstruction provided by the macrobotanical remains from the packrat middens. Cole (1990) concludes that a comparison of modern and full-glacial assemblages from the eastern GRCA packrat middens demonstrates that individual plant taxa and comparable communities shifted upward approximately 800 m at the close of the Wisconsin glacial (ca 11,000 yr B.P.). Cole (1990) concludes that the climate at the elevations of Bida and Kaetan caves was more continental during the late glacial. This result is in contradiction to the equable climates that may have occurred in western and lower-elevation regions of the GRCA and to the south of the Colorado Plateau (Mead and Phillips 1981, VanDevender 1990). Our arthropod data presented here do little to clarify the continental vs. equable climatic reconstruction contradiction. Our "cooler, moister climatic regime" reconstruction could be interpreted as a continental climate; however, it could also represent a regime with slightly cooler winters and cool summers, and therefore more available moisture.

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MICROHABITAT SELECTION BY THE JOHNNY DARTER, *ETHEOSTOMA NIGRUM* RAFINESQUE, IN A WYOMING STREAM

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ABSTRACT.—Microhabitat selection by the johnny darter (*Etheostoma nigrum*) was examined in the North Laramie River, Platte County, Wyoming, where it does not occur with other darter species in the same stream reach. Electivity indices based on microhabitat observations indicate that *E. nigrum* avoids riffles and selects certain microhabitats characterized by intermediate water depths in pools and slow-moving runs with a substrate composed primarily of silt and sand. Niche breadth and electivity values for total depth, bottom water velocity, and substrate measurements from this study indicate that *E. nigrum* is a habitat generalist, except at the extreme ends of the habitat gradient. Habitat use here is generally similar to other studies where *E. nigrum* occurred with one or more other darter species. This study found little evidence for competitive release in the absence of other darters.

Key words. microhabitat use, Percidae, niche breadth, competitive release, electivities, morphological specializations, Etheostoma nigrum.

The johnny darter exhibits the largest geographic distribution among the North American darters (Etheostomatini: Percidae), with the possible exception of *Percina caprodes*. It occurs farther west than any other darter except *Etheostoma exile* (Page 1983). The ecology of *E. nigrum* has received considerable study, often in conjunction with other darter species (e.g., Winn 1958, Smart and Gee 1979, Paine et al. 1982, Englert and Seghers 1983, Mundahl and Ingersoll 1983, Martin 1984). The ability of *E. nigrum* to colonize such a large geographic area may be explained in part by its tolerance of a variety of environmental conditions (Scott and Crossman 1973, Trautman 1981, Becker 1983).

Throughout most of its range, *E. nigrum* coexists with one or more darter species in streams (McCormick and Aspinwall 1983, Schlosser and Toth 1984, Todd and Stewart 1985). *E. nigrum* is also commonly found in lakes with weedy or sandy shorelines (Page 1983). Coexisting darters typically show resource partitioning along food and habitat axes (Smart and Gee 1979, Paine et al. 1982, Matthews et al. 1982, White and Aspinwall 1984, Todd and Stewart 1985). In addition to *E. nigrum*, the Iowa darter (*E. exile*) and the orangethroat darter (*Etheostoma spectibile*) occur in the upper Platte River drainage of eastern Wyoming. Both *E. nigrum* and *E. exile* occur in a tributary of the North Platte River, the Laramie River, and several of its tributary streams, but have not been recorded as co-occurring there (Baxter and Simon 1970, Page 1983).

The purpose of this paper is to examine the microhabitat use of *E. nigrum* at the western extreme of its range where it does not coexist with other darter species in the same reach of stream. Two basic questions are addressed: (1) Are the microhabitat requirements significantly different for *E. nigrum* in the study stream compared to other streams in North America where it is found? (2) Does *E. nigrum* show signs of competitive release in the absence of other darters?

STUDY AREA

The North Laramie River, Platte County, Wyoming, drains the central Medicine Bow Mountains and is a tributary of the Laramie River, which in turn joins the North Platte River near the town of Wheatland. The study was confined to a 100-m reach of river approximately 10 km upstream from Interstate Highway 25 (elevation 1426 m). At this location the river traverses a broad floodplain averaging 0.75–1.0 km in width. Dominant overstory riparian vegetation includes cottonwood (*Populus deltoides*) and various tree and shrub willows (*Salix* spp.). The study area is sparsely populated with large cattle ranches and alfalfa farms bordering the lower to middle reaches. The most noticeable result of these land-use practices has been removal of riparian vegetation and consequent associated sedimentation; however, fencing has effectively excluded cattle from the North Laramie River along the study reach.

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The study reach, chosen as representative of the lower portions of the North Laramie River, is generally characterized by large, relatively uniform, shallow pools connected by short riffles and runs of varying water velocities. Wetted stream channel width within the study reach averages 6.5 m with a gradient of 4.7 m/km. This contrasts with gradients within the middle reaches of the North Laramie River of 15.1 m/km. Stream discharge at the study site averages 0.17 m^3/s, although short-term fluctuations in flow may occur from summer thunderstorms and irrigation diversions. The substrate ranges from a dominance of small gravel and sand, silt, and detritus in pools to medium to large gravel and cobble in riffles and runs. Diel water temperatures in summer typically range from 13.5 to 21 C. Minimum underwater visibility in the river was 2.5 m or greater during the study. Rooted aquatic vegetation within the study reach includes waterweed (*Elodea canadensis*), perfoliate pennycress (*Thlaspi perfoliatum*), and *Ranunculus longirostris*.

METHODS

Microhabitat observations of *E. nigrum* were made 7–12 September 1988. Undisturbed fish were located by a single observer snorkeling in an upstream direction. Because of the high water clarity, relatively close spacing of individual fish, and their observed habit of remaining in direct contact with the substrate, marking the location of fish was not a problem. Typically the locations of 4–7 individuals were noted and marked by placing a white golf ball on the substrate. This approach allowed the snorkler to maximize the number of undisturbed individual observations and minimize disturbance to upstream fish.

For each individual observation the following microhabitat data were recorded: (1) total depth of the water column, (2) focal point elevation (vertical distance of the fish from the bottom), (3) focal point velocity (water velocity at the fish's snout), (4) mean water column velocity, (5) surface velocity, (6) substrate composition, and (7) cover type. Velocity measurements were made with a mini flow meter (Scientific Instruments, Inc., Model 1205). Mean water column velocity was measured as the velocity at 0.6 of the total depth when the total depth was less than 0.75 m, or the mean velocities at 0.2 and 0.8 of the total depth when greater than 0.75 m (Bovee and Milhouse 1978). Relative depth, a measurement of the location of the fish in the water column, was calculated by subtracting focal-point elevation from total depth and dividing by total depth. All observed individuals were greater than 25 mm standard length; however, no effort was made to distinguish between juvenile and adult fish.

Nine codes were used to characterize substrate composition (percentage) in an area 0.15 m on a side measured from beneath each fish: 1, fines (sand and smaller); 2, small gravel (4–25 mm); 3, medium gravel (>25–50 mm); 4, large gravel (>50–75 mm); 5, small cobble (>75–150 mm); 6, medium cobble (>150–225 mm); 7, large cobble (>225–300 mm); 8, small boulder (>300–900 mm); and 9, large boulder/bedrock (>900 mm). A cover rating (0–2) as measured by the relative degree of protection of fish from stream velocity, visual isolation, and light reduction (i.e., shading) was assigned to each observation. A rating of 0 denoted no protection; 1, moderate protection; and 2, major protection. The general type and location of cover in relation to fish also were noted.

Habitat availability was determined randomly each day immediately following the collection of microhabitat-use data (Moyle and Baltz 1985). The following availability measurements were made along 10 randomly selected transects within the study reach: total depth; bottom, mean water column, and surface velocities; substrate composition; and cover type. Between 15 and 30 equally spaced measurements were made along each transect. To adequately characterize habitat availability within the comparatively short study reach, an effort was made to collect approximately twice as many measurements of habitat availability as microhabitat observations.

An electivity index was used to determine selectivity by *E. nigrum* for total depth, bottom water velocity, and substrate composition. Electivities were calculated from the formula $D = r - p/(r + p) - 2rp$, where r is the proportion of the resource used and p is the proportion available

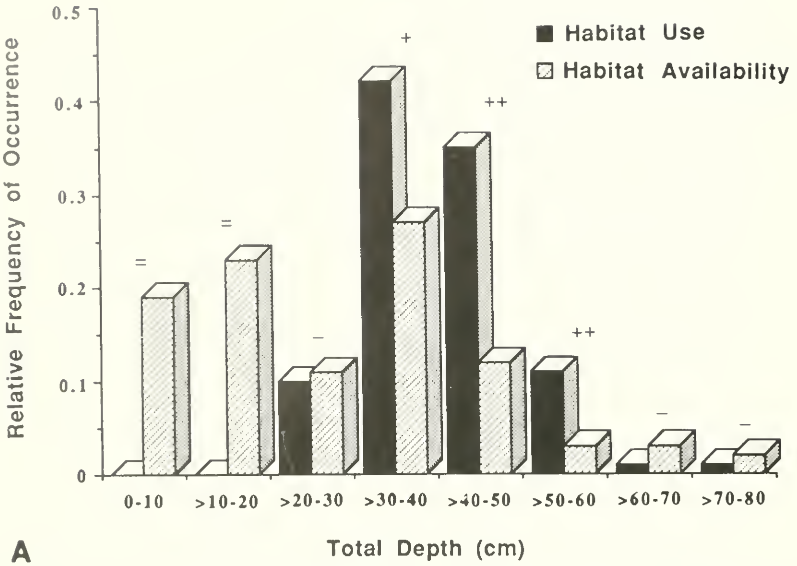

Fig. 1A. Relative frequency distributions of microhabitat use and availability for total water column depths for *E. nigrum* in the North Laramie River. Electivities are indicated ++ (>0.50, strong preference), + (>0.25 but <0.50, moderate preference), 0 (+0.25, no preference), − (> −0.05 but < −0.25, moderate avoidance), and = (< −0.05, strong avoidance).

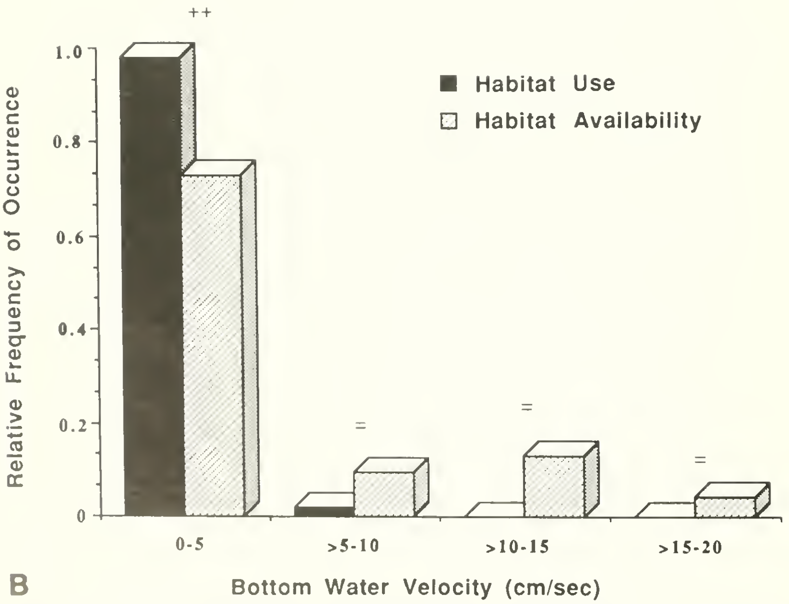

Fig. 1B. Relative frequency distributions of microhabitat use and availability for bottom water velocities for *E. nigrum* in the North Laramie River. Electivities are indicated ++ (>0.50, strong preference), + (>0.25 but <0.50, moderate preference), 0 (+0.25, no preference), − (> −0.05 but < −0.25, moderate avoidance), and = (< −0.05, strong avoidance).

in the stream environment. This index is based on the formula by Jacobs (1974), as modified by Moyle and Baltz (1985) for determining microhabitat selectivity from variables similar to those used in this study. A Kolmogorov-Smirnov test for goodness of fit was applied to frequency distributions for habitat use and availability to determine whether maximum differences between the observed and expected distributions were significant (Sokal and Rohlf 1981).

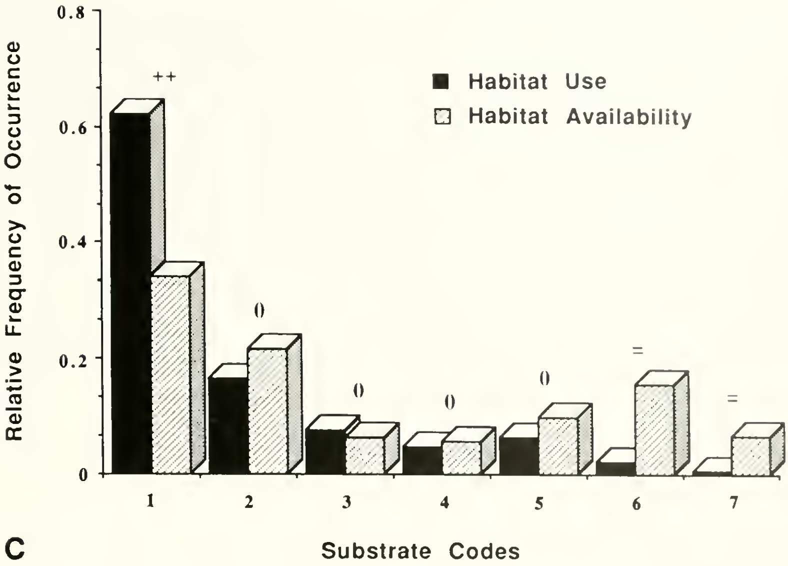

Fig. 1C. Relative frequency distributions of microhabitat use and availability for substrate codes for *E. nigrum* in the North Laramie River. Electivities are indicated ++ (>0.50, strong preference), + (>0.25 but <0.50, moderate preference), 0 (+0.25, no preference), − (>−0.05 but <−0.25, moderate avoidance), and = (<−0.05, strong avoidance).

An additional measure of microhabitat utilization, niche breadth, was calculated for E. nigrum. Two measures of niche breadth were calculated to adequately characterize the effect that the selectivity of rare and common resources might have on niche-breadth values. Hurlbert's measure of niche breadth (B′), which is sensitive to the selection of rare resources, was calculated as follows: $B' = 1/\Sigma(p_j^2/a_j)$. Smith's measure of niche breadth (*FT*), which is less sensitive to the selectivity of rare resources, was calculated as follows:

$$FT = \sum_{j=1}^{n}(\sqrt{p_j a_j})$$

where p_j equals the proportion of individuals found in resource $j(\Sigma p_j = 1.0)$, and a_j is the proportion of total available resources consisting of resource $j(\Sigma a_j = 1.0)$ (Krebs 1989). *B′* values were standardized to a scale of 0–1, using the equation $B'_A = B' - a_{min}/1 - a_{min}$, where *B′* equals Hulbert's niche breadth, and a_{min} equals the smallest observed proportion of all resources (minimum a_j). The larger the *B′* and *FT* values, the less individuals discriminate between resource states (minimum specialization); the smaller the *B′* and *FT* values, the greater the resource discrimination (maximum specialization).

RESULTS

Eight species of fish were observed with E. nigrum at the study site. These were sand shiner (*Hybognathus hankinsoni*), suckermouth minnow (*Phenacobius mirabilis*), creek chub (*Semotilus atromoculatus*), common shiner (*Notropis cornutus*), red shiner (*N. lutrensis*), bigmouth shiner (*N. dorsalis*), white sucker (*Catostomus commersoni*), and rainbow trout (*Oncorhynchus mykiss*).

Microhabitat Observations and Habitat Availability

Microhabitat-use data indicated that *E. nigrum* always occurred in continuous contact with the substrate where water velocities were low (Table 1). *Etheostoma nigrum* was almost exclusively found over a substrate of sand or small gravel, usually in pools and slow-moving runs of intermediate depth (Table 1, Figs. 1A–C). In contrast, surface velocities often were relatively high.

In this study, observations indicated that individual fish were positioned (1) on the surface of the exposed substrate with no apparent cover, (2) immediately below the front edge of a slight depression in the sand that served to protect fish from the current, or (3) rarely on the downstream slope of a small cobble also protected from the current. In all cases, *E. nigrum*

TABLE 1. Means (± S.D.) from microhabitat use and availability measurements for *E. nigrum* in the North Laramie River, Wyoming.

Variable	Habitat use observations	Habitat availability
Total depth (cm)	40.5 ± 8.8	27.1 ± 16.8
Focal point evaluation (cm)	0.1 ± 0.01	—
Relative depth (cm)	0.9 ± 0.02	—
Mean water column velocity (cm/s)	2.6 ± 4.5	3.7 ± 6.4
Focal point/bottom velocity (cm/s)	0.2 ± 0.7	1.8 ± 3.1
Surface velocity (cm/s)	5.2 ± 7.3	5.4 ± 8.2
Substrate types (%)		
(1) fines	62.1 ± 35.8	34.1 ± 36.3
(2) small gravel	16.5 ± 19.6	21.6 ± 25.6
(3) medium gravel	7.6 ± 14.7	6.4 ± 13.3
(4) large gravel	4.7 ± 13.5	5.8 ± 14.9
(5) small cobble	6.3 ± 15.7	9.7 ± 21.5
(6) medium cobble	2.1 ± 11.3	15.5 ± 28.7
(7) large cobble	0.7 ± 0.20	6.5 ± 21.5
(8) small boulder	—	—
(9) large boulder	—	—
Cover code[1] (0–2)		
Stream velocity	1.5 ± 0.6	—
Visual isolation	0.5 ± 0.6	—
Light reduction	0.1 ± 0.3	—
Sample size	91	168

[1] Refer to Methods

TABLE 2. Niche breadth values (B'_A and *FT*) for *E. nigrum* for total depth, bottom water velocity, and substrate in the North Laramie River, Wyoming (approximate 95% confidence interval shown in parentheses).

	Total depth	Bottom velocity	Substrate
Hurlbert's B'_A	.45 (.41, .49)	.76 (.72, .80)	.70 (.66, .74)
Smith's *FT*	.72 (.65, .78)	.89 (.84, .93)	.93 (.89, .96)

positioned itself in close proximity with other types of instream cover (e.g., stones, cobbles, branches, or small depressions in the sand). The average distance to such cover was less than 6 cm for 89% of the observations.

Measurements of microhabitat availability indicated that average water depths available to *E. nigrum* were shallower than the depths at which it was typically observed (Kolmogorov-Smirnov test, .23, $p < .01$), and available mean bottom water velocities were greater than where fish were observed (K-S test, .25, $p < .01$; Figs. 1A, B). In addition, available substrate was dominated by fines and small gravel (55%), but this was disproportionately low when compared with microhabitat use observations for these same substrate types (79%; K-S test, .28, $p < .01$; Fig. 1C).

Habitat Selection and Niche Breadth

Electivity indices indicate that E. nigrum was selecting certain microhabitats while avoiding others. E. nigrum selected intermediate water depths and avoided high mean water column velocities (Figs. 1A, B). There was a strong selectivity for a substrate composed of sand, and an avoidance of medium to large cobbles (Fig. 1C). Fish generally avoided areas that (1) exhibited high surface water velocities, (2) were isolated visually, or (3) were well shaded by physical cover (Table 1). Rather, fish utilized relatively barren substrates exposed to full sunlight but close to cover. Microhabitat niche breadths (B'_A and *FT* values) for depth, velocity, and substrate indicate little resource specialization by E. nigrum (Table 2).

DISCUSSION

The results of the electivity indices and the K-S test indicate that *E. nigrum* is highly selective in the microhabitats it occupies. However, niche breadth values suggest that *E. nigrum* does not discriminate between available microhabitats (i.e., minimal habitat specialization). The apparent inconsistency between niche-breadth values and electivity indices may be explained by two factors: (1) the relative scarcity in the study area of gravel/cobble riffle habitats and their avoidance by darters, and (2) the preference by darters for low-velocity pool habitats characterized by sand and small gravel, a habitat that was abundant in the study area. Values for Hurlbert's measure of niche breadth (B'_A) were consistently lower than values for Smith's measure (*FT*) for depth, velocity, and substrate. This is expected because B'_A is sensitive to the selection of rare resources that are more heavily weighted in the calculation of niche breadth, while *FT* is less sensitive to the selection of rare resources (Krebs 1989).

Darter species typically are restricted to a narrow range of microhabitats. This is especially evident in their use of certain substrates (Page 1983). *E. nigrum* has an unusually broad tolerance among darters for variable environmental conditions and has been observed over widely varying velocities, depths, and substrates between drainages and within a particular stream reach (Smart and Gee 1979, Angermeier

1987). This study and others (e.g., Becker 1959, Paine et al. 1982, Englert and Seghers 1983) generally show that *E. nigrum* occurs most frequently in pools and sluggish reaches of stream over sand or silt substrates, although this darter also regularly occurs in riffles (Lachner et al. 1950, Smart and Gee 1979, Trautman 1981). In other streams, pool and riffle habitats are often coinhabited by one or more darter species. If competition with other darter species restricts *E. nigrum* to microhabitat types in which they are commonly found, then in the absence of other darter species one might expect *E. nigrum* to experience competitive release. *Etheostoma nigrum* when alone should occupy a wider range of habitat in a particular stream reach, without as much specialization for a particular range or resource type. Observed patterns of microhabitat use from this study found little evidence of competitive release, suggesting that other darters are probably not restricting *E. nigrum* to a particular habitat type in streams where they coexist.

Electivity and niche-breadth values for depth, velocity, and substrate measurements from this study support the conclusion of Coon (1982) and others (Winn 1958, Karr 1963) that *E. nigrum* is a habitat generalist, except at the extreme ends of the habitat gradient (i.e., shallow cobble riffle and very shallow pool habitats). However, in contrast to the studies of Coon (1982) and Smart and Gee (1979), that recorded *E. nigrum* in riffle and run/pool habitats with one or more darter species, in this study *E. nigrum*, while it was common in pools, did not occur in riffles even in the absence of other darters.

Schlosser and Toth (1984) suggested that differences in microhabitat use in two sympatric darters appear to be constrained by morphological specializations of each species rather than by interspecific competition. As with most small darters, *E. nigrum* is characterized by morphological specializations best suited to the benthic stratum of pools and other sluggish stream habitats, often with a sand or silt substrate (Page 1983, Page and Swofford 1984). Support for the role of morphology in driving habitat utilization by *E. nigrum* in the study area comes from data on cover utilization. Protection from stream velocities in the absence of any apparent physical instream cover may be explained by this species' small size and benthic habits. Velocities immediately above the substrate where fish were observed were negligible when compared to velocities at the same location a few centimeters higher in the water column or at the surface. Also, subtle depressions in the sand substrate often were occupied by individual fish presumably for protection from stream velocity. One might expect that the small size and observed patterns of habitat utilization by *E. nigrum* would increase its risks to predation. However, small size, drab coloration, speckling, W-marks, and partial translucence, combined with exposure to full sunlight, made detection of individual fish on the speckled sand substrate difficult. The increased risks of exposure to predation from small size alone would appear to be compensated by the combination of various morphological features. The same morphological features that act as camouflage in quiet pools likely may not serve the same function in riffle habitats (Page and Swofford 1984).

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NOMENCLATURAL INNOVATIONS IN INTERMOUNTAIN ROSIDAE

Arthur Cronquist[1, 2]

ABSTRACT.—New taxa include *Lomatium packardiae* Cronq. (Apiaceae), *Croton texensis* (Klotzsch) Muell. Arg. var. *utahensis* Cronq. (Euphorbiaceae). Other nomenclatural innovations include: *Cymopterus longipes* var. *ibapensis* (M. E. Jones) Cronq., *Lomatium roseanum* Cronq. (Apiaceae); *Camissonia boothii* (Douglas) Raven var. *decorticans* (Hook. & Arn.) Cronq., *Camissonia boothii* (Douglas) Raven var. *desertorum* (Munz) Cronq., *Camissonia claviformis* (Torr. & Frém.) Raven var. *aurantiaca* (Munz) Cronq., *Camissonia claviformis* (Torr. & Frém.) Raven var. *cruciformis* (Kellogg) Cronq., *Camissonia claviformis* (Torr. & Frém.) Raven var. *funerea* (Raven) Cronq., *Camissonia claviformis* (Torr. & Frém.) Raven var. *lancifolia* (A. A. Heller) Cronq., *Camissonia heterochroma* (S. Wats.) Raven var. *monoensis* (Munz) Cronq., *Camissonia kernensis* (Munz) Raven var. *gilmanii* (Munz) Cronq., *Camissonia scapoidea* (Torr. & Gray) Raven var. *macrocarpa* (Raven) Cronq., *Oenothera biennis* L. var. *strigosa* (Rydb.) Cronq., *Oenothera pallida* Lindl. var. *runcinata* (Engelm.) Cronq. (Onagraceae).

Key words: nomenclature, Rosidae, taxonomy.

My manuscript on a number of families of Rosidae for Intermountain Flora has been completed and awaiting publication for several years. These families should constitute a large part of volume 3A (Rosidae except Fabales). Since I cannot now anticipate when volume 3A will be published, the following nomenclatural innovations are here validated.

APIACEAE

***Cymopterus longipes* S. Wats. var. *ibapensis* (M. E. Jones) Cronq.,** comb. nov. [based on: *Cymopterus ibapensis* M. E. Jones, Zoe 3: 302. 1893].

***Lomatium packardiae* Cronq.,** sp. nov. (Fig. 1). Herba perennia caespitosa radice crasse et candice manifeste ramoso, omnino subvelutina, foliis omnibus basalibus, ternato (vel quinato)-pinnatifida et denuo plus-minusve pinnatifidis, segmentis ultimis angustis, 1–2 mm latis, imparibus, eis majoribus 1–3 cm longis; scapi maturi 1.5–4 dm alta, umbella per anthesin compacta, parva, ca 2 cm lata, radiis imparibus, demum aperta radiis longioribus 4–6 cm longis, bracteis involucelli paucis, lineari-attenuatis vel nullis; flores flavi, lobis calycis minutis vel obsoletis; pedicelli fructiferi 3–7 mm longi; mericarpia glabra vel interdum patenti-hirtella, 8–9 × 3–3.5 mm, manifeste alata, alis usque ad 1 mm latis.

HOLOTYPE.—*Packard 74-46*, in ash that has not disintegrated into clay, along Old Succor Creek Road, near Sheaville, very close to the Idaho border, T27S, R46E, Malheur Co., Oregon, 19 May 1974; NY! Isotype at CIC!

HABITAT AND DISTRIBUTION.—In volcanic ash and rhyolite on rocky clay soil in the sagebrush zone. Malheur and Lake cos., Oregon, S to Washoe and Humboldt cos., Nevada. Flowering from April to June.

COMMENTARY.—*Lomatium packardiae* has sometimes passed in the herbarium as *L. triternatum* (Pursch) Coulter & Rose, which however has solitary or few stems or scapes on the simple or occasionally few-branched crown or short caudex atop the taproot. The ultimate segments of the leaves of *L. packardiae* are also shorter than is typical for *L. triternatum*, the larger ones only 1–3 cm long, so that the leaves have a different aspect.

***Lomatium roseanum* Cronq.,** nom. nov. *Leptotaenia leibergii* Coulter & Rose, Contrib. U.S. Natl. Herb. 7: 202. 1900. Not *Lomatium leibergii* Coulter & Rose, 1900.

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[1] The New York Botanical Garden, Bronx, New York 10458-5126.

[2] Deceased March 22, 1992.

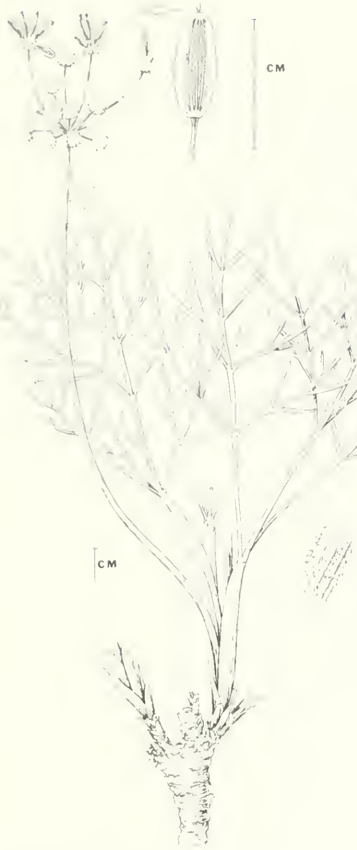

Fig. 1. *Lomatium packardiae.*

EUPHORBIACEAE

Croton texensis (Klotzsch) Muell. Arg. var. *utahensis* Cronq., var. nov. A var. texensis foliis supra glabris differt.

HOLOTYPE.—*Cronquist & K. Thorne 11839*, sand dunes ca 18 km airline N of Lynndyl, Juab Co., Utah, T13S, R5W, ca 1500 m elev., 28 July 1983, at NY! Isotypes at BRY!, UTC!

COMMENTARY.—*Croton texensis* is variable in density of pubescence, but throughout most of its range the upper surface of the leaves has at least a few stellate hairs (though these may eventually fall off). An abundant population on the sand dunes near Lynndyl in Juab and Millard cos., Utah, represents the least pubescent extreme. In these plants the upper surface of the leaves is wholly glabrous or provided with only a few quickly deciduous stellate scales. The Lynndyl plants and some similar ones from Kane and San Juan cos., Utah, and from northern Coconino Co. in Arizona, are here considered to form the var. *utahensis* Cronq. The otherwise fairly widespread var. *texensis*, with the upper surface of the leaves evidently (and more or less persistently) stellate-hairy, is largely allopatric with var. *utahensis*, barely entering Utah in San Juan Co.

ONAGRACEAE

Camissonia boothii (Douglas) Raven var. *decorticans* (Hook. & Arn.) Cronq., comb. nov. [based on: *Gaura decorticans* Hook. & Arn. Bot. Beechey's Voyage 343. 1839].

Camissonia boothii (Douglas) Raven var. *desertorum* (Munz) Cronq., stat. nov. [based on: *Oenothera decorticans* var. *desertorum* Munz, Bot. Gaz. 85: 246. 1928].

Camissonia clavaeformis (Torr. & Frém.) Raven var. *aurantiaca* (Munz) Cronq., stat. nov. [based on: *Oenothera scapoidea* var. *aurantiaca* S. Wats. Proc. Amer. Acad. Arts 8: 595, 613. 1873; an illegitimate name which as defined by Watson included the type of the earlier *O. scapoidea* var. *clavaeformis* S. Wats. 1871. *Oenothera clavaeformis* var. *aurantiaca* Munz, Amer. J. Bot. 15: 237. 1928].

Camissonia clavaeformis (Torr. & Frém.) Raven var. *cruciformis* (Kellogg) Cronq., stat. nov. [based on: *Oenothera cruciformis* Kellogg, Proc. Calif. Acad. Sci. 2: 227. 1863].

Camissonia clavaeformis (Torr. & Frém.) Raven var. *funerea* (Raven) Cronq., stat. nov. [based on: *Oenothera clavaeformis* subsp. *funerea* Raven, Univ. Calif. Pub. Bot. 34: 106. 1962].

Camissonia clavaeformis (Torr. & Frém.) Raven var. *lancifolia* (A. A. Heller) Cronq., stat. nov. [based on: *Chylismia lancifolia* A. A. Heller, Muhlenbergia 2: 226. 1906].

Camissonia heterochroma (S. Wats.) Raven var. *monoensis* (Munz) Cronq., stat. nov. [based on: *Oenothera heterochroma* var. *monoensis* Munz, Aliso 2: 84. 1949].

Camissonia kernensis (Munz) Raven var. *gilmanii* (Munz) Cronq., stat. nov. [based on: *Oenothera dentata* var. *gilmanii* Munz, Leafl. W. Bot. 2: 87. 1938].

Camissonia scapoidea (Torr. & Gray) Raven var. *macrocarpa* (Raven) Cronq., stat nov. [based on: *Oenothera scapoidea* subsp. *macrocarpa* Raven, Univ. Calif. Pub. Bot. 34: 95. 1962].

***Oenothera biennis* L. var. *strigosa* (Rydb.) Cronq.**, comb. nov. [based on: *Oenothera strigosa* Rydb. Mem. N. Y. Bot. Gard. 1: 278. 1900].

***Oenothera pallida* Lindl. var. *runcinata* (Engelm.) Cronq.**, stat. nov. [based on: *Oenothera albicaulis* var. *runcinata* Engelm. Amer. J. Sci. Arts 84: 334. 1862].

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NOMENCLATURAL CHANGES AND NEW SPECIES IN PLATYPODIDAE AND SCOLYTIDAE (COLEOPTERA), PART II

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ABSTRACT.—In Platypodidae the new name *Genyocerus strohmeyeri* replaced the junior homonym *G. albipennis* Strohmeyer, 1942, and the new name *Platypus applanatulus* replaced the junior homonym *Platypus applanatus* Schedl, 1976. New names are presented in Scolytidae as replacements for junior homonyms as follows: *Cryphalus brownei* for *Cryphalus artocarpus* Schedl, 1958; *Cyclorhipidion dihingicum* for *Xyleborus dihingensis* Schedl, 1951; *Hypothenemus aterrimulus* for *Lepiceroides* (now *Hypothenemus*) *aterrimus* Schedl, 1957; *Hypothenemus krivolutskayae* for *Hypothenemus insularis* Krivolutskaya; *Pityophthorus africanulus* for *Neodryocoetes* (now *Pityophthorus*) *africanus* Schedl, 1962; *Scolytogenes papuensis* for *Xylocryptus* (now *Scolytogenes*) *papuanus* Schedl, 1975; *Scolytogenes paradoxus* for *Scolytogenes papuanus* Schedl, 1979; *Xyleborinus spiniposticus* for *Eidophelus* (now *Xyleborinus*) *spinipennis* Schedl, 1979; *Xyleborus formosae* for *Xyleborus formosanus* Browne, 1981. New combinations for fossil Scolytidae include *Dryocoetes diluvialis* for *Pityophthoroidea diluvialis* Wickham, 1916, and *Hylesinus hydropicus* for *Apidocephalus hydropicus* Wickham, 1916. *Phloeotribus zimmermanni* Wickham, 1916, is transferred to the family Curculionidae. In Scolytidae, *Cryphalophilus* Schedl, 1970, is a junior generic synonym of *Scolytogenes* Eichhoff; *Macrocryphalus* Nobuchi, 1981, is a junior generic synonym of *Hypothenemus* Westwood, 1836; *Nipponopolygraphus* Nobuchi, 1981, is a junior generic synonym of *Polygraphus* Erichson, 1836; *Pseudocosmoderes* Nobuchi, 1981, is a junior generic synonym of *Cosmoderes* Eichhoff, 1878; *Taphrocoetes* Pfeffer, 1987, is a junior generic synonym of *Taphrorychus* Eichhoff; *Trypanophellos* Bright, 1982, is a junior generic synomym of *Liparthrum* Wollaston. New specific synonymy in Scolytidae includes: *Brachyspartus moritzi* Ferrari (=*Corthylus obtusus* Schedl), *Carphoborus minimus* (Fabricius) (=*Carphoborus balgensis* Murayama), *Coccotrypes dactyliperda* (Fabricius) (=*Coccotrypes tropicus* Eichhoff), *Cryphalus scabricollis* Eichhoff (=*Cryphalus brevicollis* Schedl), *Ficicis despects* (Walker) (=*Hylesinus samoanus* Schedl), *Hylastes plumbeus* Blandford (=*Hylurgops fushunensis* Murayama), *Hylurgops interstitialis* (Chapuis) (=*Hylurgops niponicus* Murayama), *Hylurgops spessivtsevi* Eggers (=*Hylurgops modestus* Murayama), *Ips stebbingi* Strohmeyer (=*Ips schmutzenhoferi* Holzschuh), *Phloeosinus rudis* Blandford (=*Phloeosinus shotoensis* Murayama, *Polygraphus kaimochi* (Nobuchi) (=*Polygraphus querci* Wood), *Polygraphus proximus* Blandford (=*Polygraphus magnus* Murayama), *Scolytogenes braderi* Browne (=*Scolytogenes orientalis* Schedl), *Scolytoplatypus parvus* Sampson (=*Scolytoplatypus ruficauda* Eggers), *Sphaerotrypes querci* Stebbing (=*Chramesus globulus* Stebbing, *Sphaerotrypes tectus* Beeson), *Sueus niisimai* (Eggers) (=*Sphaerotrypes controversae* Murayama), *Tomicus brevipilosus* (Eggers) (=*Blastophagus khasianus* Murayama, *Blastophagus multisetosus* Murayama). The European *Hylastes opacus* Erichson is reported as an established breeding population in New York (USA). *Phloeosinus armatus* Reitter of Asia Minor is reported as causing economic damage as a new introduction to Los Angeles County, California. The following species are named as new to science: *Cyclorhipidion subagnatum* (Philippine Islands), *Dendrotrupes zealandicus* (New Zealand), *Polygraphus thitsi* (Burma), *Triotemnus pilicornis* (India), and *Xyleborus magnificus* (Peru).

Key words: nomenclature, Platypodidae, Scolytidae, taxonomy, bark beetles, Coleoptera.

During the compilation of a world catalog of Platypodidae and Scolytidae, a number of nomenclatural items were found that require validation and/or publication prior to release of the catalog. These items include: (a) two new replacement names for junior homonyms in Platypodidae and nine in Scolytidae, (b) three new combinations in fossil Scolytidae, (c) six cases of new generic synonymy in Scolytidae, (d) 17 cases of new specific synonymy in Scolytidae, (e) two new introductions of a European and an Asian scolytid into North America, and (f) five species named as new to science.

NEW NAMES IN PLATYPODIDAE

Genyocerus strohmeyeri, n. n.

Diapus albipennis Strohmeyer, 1942, Arbeiten uber Morphologische und Taxonomische Entomogie 9:284 (Syntypes: Insul Simaloer, westlich Sumatra; Strohmeyer Collection), preoccupied by Motschulsky, 1858

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The name *Genyocerus albipennis* Motschulsky, 1858, was considered lost for more than a century (Wood 1969:118). In an attempt to assign a species to this name, Strohmeyer named *Diapus albipennis*, cited above. When the Motschulsky type was rediscovered (Wood 1969:118), it was recognized that two distinct but congeneric species were represented. Because the Strohmeyer name is the junior homonym in this case, the new name *strohmeyeri* is proposed as a replacement name for *albipennis* Strohmeyer, as indicated above.

Platypus applanatulus, n. n.

Platypus applanatus Schedl, 1976, Abhandlungen Staatliches Museum fur Tierkkunde Dresden 41(3):85 (Holotype, male; Manaus, Amazonas; Naturhistorisches Museum Wien), preoccupied by Wood, 1972

Platypus applanatus Schedl, 1976, cited above, was named five years after the same name had been used by Wood (1972:244). In view of this homonymy, the new name *applanatulus* is here proposed as a replacement for the junior name *applanatus* Schedl, as indicated above.

NEW NAMES IN SCOLYTIDAE

Cryphalus brownei, n. n.

Cryphalus artocarpus Schedl, 1958, Sarawak Museum Journal 8(11):498 (Holotype; Sarawak, Semengoh; British Museum [Natural History]), preoccupied by Schedl, 1939

The name *Cryphalus artocarpus* Schedl, 1958, cited above, was established even though its author had previously named *Ericryphalus artocarpus* Schedl, 1939, and had considered *Cryphalus* and *Ericryphalus* synonymous. This generic synonymy was confirmed (Wood 1986:91). In view of this oversight, Schedl's 1958 name is a junior homonym of the 1939 name and must be replaced. The new name *brownei* is proposed as a replacement, as indicated above, in recognition of the late F. G. Browne who contributed significantly to our knowledge of these insects.

Cyclorhipidion dihingicum, n. n.

Xyleborus dihingensis Schedl, 1951, Tijdschrift voor Entomologie 93:71 (Syntypes, 2 females, 1 male; Java: Batoerraden, G. Slamet; Naturhistorisches Museum Wien), preoccupied by Eggers 1930

The name *Xyleborus dihingensis* Schedl, cited above, was proposed at a time when it was preoccupied by Eggers, 1930. Although both names were recently transferred to other genera, the primary homonymy remains. The new name *dihingicum* is proposed as a replacement for the Schedl name as indicated above.

Hypothenemus aterrimulus, n. n.

Lepiceroides aterrimus Schedl, 1957, Annales du Musée Royale du Congo Belge, ser. 8, Zoologie 56:59 (Holotype; Ruanda: Ihembe; Belgian Congo Museum, Tervuren), preoccupied by Schedl, 1951

The generic name *Lepiceroides* Schedl was placed in synonymy under *Hypothenemus* (Wood 1986:92). This act transferred its type-species, *aterrimus* Schedl, 1957, cited above, to *Hypothenemus* where it became a junior homonym of *H. aterrimus* (Schedl, 1951). The new name *aterrimulus* is here proposed as a replacement name for *aterrimus* Schedl, 1957, as indicated above.

Hypothenemus krivolutskayae, n. n.

Hypothenemus insularum Krivolutskaya, 1968, *in* Kurenzov & Konoralova. The insect fauna of the Soviet Far East and its ecology, p. 56 (Holotype; Kurile Islands; presumably at Vladivostok), preoccupied by Perkins, 1900

Hypothenemus insularum Krivolutskaya, cited above, was given a neuter specific name in a masculine genus. When the gender is corrected, as required under the Code, this name becomes a junior homonym of *Hypothenemus insularis* Perkins, 1900, and must be replaced. The new name *krivolutskayae* is proposed as a replacement name, as indicated above.

Pityophthorus africanulus, n. n.

Neodryocoetes africanus Schedl, 1962, Revista de Entomologia de Moçambique 5(2):1079 (Holotype, Congo: Mayumbe; Belgian Congo Museum, Tervuren), preoccupied by Eggers, 1927

Schedl named *Neodryocoetes africanus*, cited above, from five specimens that did not exhibit sexual differences. Because the neotropical genus *Araptus* (=*Neodryocoetes*) does not occur in Africa and these specimens belong to the related genus *Pityophthorus*, Schedl's name, *africanus*, must be transferred to that genus where it becomes a junior homonym and must be replaced. The new name *africanulus* is proposed as a replacement for the 1962 Schedl name as indicated above.

Scolytogenes papuensis, n. n.

Xylocryptus papuanus Schedl, 1975, Naturhistorisches Museum Wien, Annales 79:352 (Holotype: Upper Manki logging area, Bulolo, Morobe District, New Guinea; Naturhistorisches Museum Wien), preoccupied by Schedl, 1974

The genus *Xylocryptus* Schedl, 1975, was established with *X. papuanus* Schedl as the type-species. When *Xylocryptus* became a junior synonym of *Scolytogenes* (Wood 1986:90), the transfer of *papuanus* to that genus caused *papuanus* Schedl, 1975, to become a junior homonym of *Scolytogenes* (originally *Cryphalomorphus*) *papuanus* (Schedl, 1974). In order to correct this duplication of names, the new name *papuensis* is here proposed as a replacement for *papuanus* Schedl, 1975, as indicated above.

Scolytogenes paradoxus, n. n.

Scolytogenes papuanus Schedl, 1979, Faunistische Abhandlungen 7:97 (Holotype; Papua, New Guinea; Naturhistorisches Museum Wien), preoccupied by Schedl, 1974

When *Scolytogenes papuanus* Schedl, 1979, was named, Schedl regarded *Cryphalomorphus* as a distinct genus. The placement of *Cryphalomorphus* in synonymy under the senior name *Scolytogenes* (Wood 1986:90) and the consequent transfer of *C. papuanus* Schedl, 1974, to *Scolytogenes* caused the name *S. papuanus* Schedl, 1979, to become a junior homonym. For this reason, the new name *paradoxus* is proposed as a replacement for *papuanus* Schedl, 1979, as indicated above.

Xyleborinus spiniposticus, n. n.

Eidophelus spinipennis Schedl, 1979, New Zealand Entomologist 7:106 (Holotype, female?; Fiji; Schedl Collection in Naturhistorisches Museum Wien), preoccupied by Eggers, 1930

Beaver (1990:94) transferred *Eidophelus spinipennis* Schedl, 1979, to *Xyleborinus* where it is preoccupied by *spinipennis* (Eggers, 1930). In order to remove the duplication of names, the new name *spiniposticus* is here proposed as a replacement for *spinipennis* (Schedl, 1979) as indicated above.

Xyleborus formosae, n. n.

Xyleborus formosanus Browne, 1981, Kontyu 49(1):131 (Holotype, female; Hualien (Formosa) to Yatsushiro (Japan) imported, British Museum [Natural History]), preoccupied by Eggers 1930

When Browne named *Xyleborus formosanus*, cited above, he overlooked previous usage of this species-group name in the combination *Xyleborus mancus formosanus* Eggers, 1930:186. Because the Browne name is a junior homonym, it must be replaced. The new name, *formosae*, is proposed as a replacement as indicated above.

GENERIC TRANSFERS OF FOSSIL SCOLYTIDAE

Dryocoetes diluvialis (Wickham)

Pityophthoridea diluvialis Wickham, 1916, State University of Iowa, Laboratory of Natural History, Bulletin 7:18 (Holotype; fossil in Miocene, Florissant, Colorado; not located)

The photograph of the holotype that was published with the original description of *Pityophthoridea diluvialis* Wickham (1916:18) suggests that this species is a member of the genus *Dryocoetes*. Because there appears to be no justification whatever for recognizing a separate genus, the name *Pityophthoroides* is placed in synonymy under the senior name *Dryocoetes*, and *diluvialis* is transferred to that genus, as indicated above.

Hylesinus hydropicus (Wickham)

Apidocephalus hydropicus Wickham, 1916, State University of Iowa, Laboratory of Natural History, Bulletin 7:18 (Holotype; fossil in Miocene, Florissant, Colorado; not located)

The photograph of the holotype that was published with the original description of *Apidocephalus hydropicus* Wickham indicates that this species is a member of the genus *Hylesinus*. The generic name *Apidocephalus* is here placed in synonymy under *Hylesinus* and the fossil species *hydropicus* is transferred to that genus, as indicated above.

Phloeotribus zimmermanni Wickham, to Curculionidae

Phloeotribus zimmermanni Wickham, 1916, State University of Iowa, Laboratory of Natural History, Bulletin 7:19 (Holotype; fossil in Miocene, Florissant, Colorado; not located)

The photograph of the holotype of *Phloeotribus zimmermanni* Wickham (1916:19) that was published with the original description indicates that this species is not a member of this family and must be transferred from Scolytidae to the family Curculionidae.

NEW SYNONYMY IN SCOLYTIDAE

Cosmoderes Eichhoff

Cosmoderes Eichhoff, 1878, Société Entomologique de Liége, Memoires (2)8:495 (Type-species: *Cosmoderes monilicollis* Eichhoff, monobasic)

Pseudocosmoderes Nobuchi, 1981, Kontyu 49(1):16 (Type-species: *Pseudocosmoderes attenuatus* Nobuchi =*Cosmoderes monilicollis* Eichhoff, original designation). *New synonymy*

The genus *Pseudocosmoderes* Nobuchi, cited above, was named for *Pseudocosmoderes attenuatus* Nobuchi, 1981. The photograph of the type material that accompanied the original description is an illustration of *Cosmoderes monilicollis* Eichhoff, 1878. The Nobuchi genus is an obvious synonym of *Cosmoderes*. The specific synonymy requires confirmation, but is almost certainly correct.

Dryocoetes Eichhoff

Dryocoetes Eichhoff, 1864, *in* Schrenk, Riesen und Forschungen in Amur-Lande 2:155 (Type-species: *Bostrichus autographus* Ratzeburg, subsequent designation by Wood 1974)

Pityophthoridea Wickham, 1916, State University of Iowa, Laboratory of Natural History, Bulletin 7:18, figs. 27–28 (Type-species: *Pityophthoridea diluvialis* Wickham, original designation). *New synonymy*

The figures of the holotype of *Pityophthoridea* that were published with the original description indicate that the type-species, *P. diluvialis*, is a member of the genus *Dryocoetes*. Consequently, Wickham's name *Pityophthoridea* is placed in synonymy under the senior name, as indicated above.

Hypothenemus Westwood

Hypothenemus Westwood, 1836, Entomological Society of London, Transactions 1:34 (Type-species: *Hypothenemus eruditus* Westwood, monobasic)

Macrocryphalus Nobuchi, 1981, Kontyu 49(1):14 (Type-species: *Macrocryphalus oblongus* Nobuchi, original designation). Probable synonymy

The genus *Macrocryphalus* Nobuchi, cited above, was named for *Macrocryphalus oblongus* Nobuchi. A close examination of the photographs of type material published with the original descriptions clearly indicates that the species *oblongus* is composite. The "male" illustrated is a female of *Hypothenemus fuscicollis* Eichhoff, a species rapidly becoming pantropical in distribution through commerce. The "female" is a female of another *Hypothenemus* species that cannot be identified with certainty from the illustrations. It represents an obvious introduction from another area. The name *Macrocryphalus* is here placed in synonymy until the name *oblongus* can be clarified.

Liparthrum Wollaston

Liparthrum Wollaston, 1854. Insecta Maderensia, p. 294 (Type-species: *Liparthrum bituberculatum* Wollaston, original designation)

Trypanophellos Bright, 1982, Studies on Neotropical Fauna and Environment 17:166 (Type-species: *Trypanophellos necopinus* Bright). *New synonymy*

Trypanophellos necopinus Bright was based on a unique female collected by Schwarz at Cayamas, Cuba. I examined this specimen in 1976 at the U.S. National Museum and recognized it as a distinctive, undescribed species of *Liparthrum*. The holotype was recently reexamined and compared to other *Liparthrum* species. Because I am unable to see any generic characters that might possibly distinguish *Trypanophellos* from *Liparthrum*, Bright's generic name is placed in synonymy under the senior name as indicated above. The species, *L. necopinus*, is unique among American *Liparthrum* species in having a double row of scales on the declivital interstriae.

Polygraphus Erichson

Polygraphus Erichson, 1836, Archiv für Naturgeschichte 2(1):57 (Type-species: *Hylesinus pubescens* Fabricius =*Dermestes poligraphus* Linneaus, monobasic)

Nipponopolygraphus Nobuchi, 1981, Kontyu 49:12 (Type-species: *Nipponopolygraphus kaimochi* Nobuchi original designation). *New synonymy*

The holotype and two paratypes of *Nipponopolygraphus kaimochi* Nobuchi were examined and found to be normal specimens of *Polygraphus* Erichson in which the eye is deeply emarginate, but not divided. Approximately one-fifth of the species in this genus have the halves of the eye connected. The Nobuchi genus was based on this one unusable character and must be placed in synonymy as indicated above.

Scolytogenes Eichhoff

Scolytogenes Eichhoff, 1878, preprint of Société Royale des Sciences de Liége, Memoires (2)8:475, 479 (Type-species: *Scolytogenes darwini* Eichhoff, monobasic)

Cryphalophilus Schedl, 1970, Kontyu 38:358 (Type-species: *Cryphalophilus afer* Schedl, monobasic). *Correction of synonymy*

Due to a clerical error in Wood (1984:228), the name *Cryphalophilus* Schedl was incorrectly placed in synonymy under the name *Scolytodes*, a neotropical genus. *Cryphalophilus* is actually a synonym of *Scolytogenes*, a circumtropical genus. The holotype of the type-species, *C. afer*, was examined.

Taphrorychus Eichhoff

Taphrorychus Eichhoff, 1878, preprint of Société Royale des Sciences de Liége, Memoires (2)8:49, 204 (Type-species: *Bostrichus bicolor* Herbst, subsequent designation by Hopkins 1914)

Taphrocoetes Pfeffer, 1987. Acta Entomologica Bohemoslovaca 82:22 (Type-species: *Taphrorychus hirtellus* Eichhoff, original designation). *New synonymy*

The name *Taphrocoetes* Pfeffer, cited above, was proposed as a means to subdivide the genus *Taphrorychus* using the size and distribution of asperities on the anterior slope of the pronotum. Because *Taphrorychus* is much more widespread and diverse (Wood 1986:74) than was known to Pfeffer, a division of the genus using the pronotal characters he proposed is not possible or meaningful. Several examples of all European and most Asiatic species of this genus were examined in my review of this problem. As indicated above, *Taphrocoetes* is placed in synonymy under the senior name.

Brachyspartus moritzi Ferrari

Brachyspartus moritzi Ferrari, 1867, Die Forst- und Baumzuchtschadlichen Borkenkafer, p. 68 (Holotype, female; Venezuela; Naturhistorisches Museum Wien)

Corthylus obtusus Schedl, 1966, Entomologsche Arbeiten aus der Museum Frey 17:122 (Holotype, female; Venezuela; Naturhistorisches Museum Wien). *New synonymy*

The female holotypes of *Brachyspartus moritzi* Ferrari and *Corthylus obtusus* Schedl were compared directly to one another by me and were found to be identical in all respects. They obviously represent one species in which Ferrari's name has priority, as indicated above.

Carphoborus minimus (Fabricius)

Hylesinus minimus Fabricius, 1801, Systema Eleutheratorum 1:395 (Syntypes, 4; Saxoniae; Copenhagen Museum)

Carphoborus balgensis Murayama, 1943, Annotationes Zoologicae Japonenses 22:99 (Lectotype, male; District of Balga, Manchoukuo, China; U.S. National Museum, present designation). *New synonymy*

Carphoborus balgensis Murayama was named from one male and one female syntypes mounted on separate microcards on one pin. The male is in recognizable condition and is here designated as the lectotype for this Murayama name. The "female" has been damaged and only the head remains; its face is entirely immersed in glue. This lectotype was compared to males of my series of *C. minimus* (Fabricius) from Europe and northern Asia. While no two males of this species are ever exactly the same, the *balgensis* lectotype is of the same size and proportions as *C. minimus* and falls well within the limits of variability and geographical range for this species. Because only one species is represented by this material, the name *balgensis* is placed in synonymy as indicated above.

Coccotrypes dactyliperda (Fabricius)

Bostrichus dactyliperda Fabricius, 1801, Systema Eleutheratorum 2:387 (Syntypes, female; date pits intercepted in Europe; Copenhagen Museum)

Coccotrypes tropicus Eichhoff, 1878, preprint of Société Royale des Sciences de Liége, Memoires (2)8:312 (Holotype, female; America Meridionalis (Peru); Hamburg Museum, lost). *New synonymy*

Eichhoff states in the original description, cited above, that his *Coccotrypes tropicus* is near *C. dactyliperda*. Because the description fits the pantropical *dactyliperda*, because there are no known endemic *Coccotrypes* in South America, and because the unique holotype and only known specimen of *tropicus* was lost in the destruction of the Hamburg Museum, *C. tropicus* is here placed in synonymy under the senior name, as indicated above, as a means of dealing with this unidentifiable species.

Cryphalus scabricollis Eichhoff

Cryphalus scabricollis Eichhoff, 1878, preprint of Société Royale des Sciences de Liége, Memoires (2)8:36 (Holotype; Hindustan Asiae; Hamburg Museum, lost)

Cryphalus brevicollis Schedl, 1943, Entomologische Blätter 39(1–2):36 (Lectotype, female; Baguio, Luzon, Philippinen; Naturhistorisches Museum Wien, designated by Schedl 1979:47). *New synonymy*

The holotype of *Cryphalus scabricollis* Eichhoff was lost in the 1944 destruction of the Hamburg Museum. My concept of this species is based on a series of specimens in the Forest Research Institute, Dehra Dun, that was compared by Beeson and Eggers to the holotype before it was lost. My series was compared directly by me to this series; then these specimens were later compared to the holotype of *C. brevisetosus* Schedl. All represent the same common, widely distributed species that infests various species of *Ficus* from India to the Philippine Islands. For this reason, Schedl's name *C. brevisetosus* is here placed in synonymy under the senior name, as indicated above.

Ficicis despectus (Walker)

Hylesinus despectus Walker, 1859, Annals and Magazine of Natural History (3)3:261 (Holotype; Ceylon; British Museum [Natural History])

Hylesinus samoanus Schedl, 1951, Bishop Museum Occasional Papers 20(10):142 (Syntypes, male; Upolu, Tapatapao; British Museum [Natural History] and Naturhistorisches Museum Wien). *New synonymy*

The Schedl syntypes of *Hylesinus samoanus* Schedl in the Wien Museum were examined by me and were compared directly to my homotypes of *H. despectus* Walker. Only one species was recognized. On the basis of this comparison, Schedl's name is placed in synonymy, as indicated above.

Hylastes plumbeus Blandford

Hylastes plumbeus Blandford, 1894, Entomological Society of London, Transactions 1894:57 (Syntypes; Nagasaki et a Hioga, Japan; Brussels Museum)

Hylurgops fushunensis Murayama, 1940, Annotationes Zoologicae Japonensis 19:235 (Lectotype, female; Fushen, Manchuria; U.S. National Museum, present designation). *New synonymy*

Hylurgops fushunensis Murayama was based on one male and one female syntypes that are mounted on one pin. The callow female is mounted upright; the callow male is mounted upside down with the dorsal surface imbedded in glue. The female is here designated as the lectotype for *H. fushunensis* Murayama. This lectotype was compared directly to my Ussuri specimens of *Hylastes plumbeus* Blandford that were identified by Kurenzov. These specimens clearly represent one species. For this reason, *fushunensis* is transferred to *Hylastes* and is placed in synonymy under the senior name, as indicated above.

Hylurgops interstitialis (Chapuis)

Hylastes interstitialis Chapuis, 1875, Société Entomologique Belgique, Annales 18:196 (Syntypes; Nagasaki and Kiushu, Japan; Brussels Museum)

Hylurgops niponicus Murayama, 1936, Tenthredo 1:123, 149 (Holotype, male; Kamikochi, Nagano prefecture; U.S. National Museum). *New synonymy*

The unique male holotype of *Hylurgops niponicus* Murayama was examined and compared directly to my long series of *H. interstitialis* (Chapuis) from Japan (determined by Nobuchi) and Siberia (determined by Kurenzov). The Murayama holotype is an average Japanese specimen of this species. The name *niponicus* is here placed in synonymy under the senior name as indicated above.

Hylurgops spessivtsevi Eggers

Hylurgops spessivtsevi Eggers, 1914, Entomologische Blätter 10:187 (Lectotype, male; Ostsiberien, USSR; U.S. National Museum, designated by Anderson & Anderson 1971:30)

Hylurgops modestus Murayama, 1937, Tenthredo 1:367 (Syntypes; Pic Biro du Kongosan, Korea; Murayama Collection in U.S. National Museum). *New synonymy*

Two female specimens in the Murayama Collection are labeled as "paratypes" of *Hylurgops modestus* Murayama. Their label indicates that they were taken at "Yalelomia, Manchuria, 25-VIII-1940 by A. Takagi"; a second label gives "Manchoukuo, Collected 1940, J. Murayama, *Hylurgops modestus* Murayama, paratype." Because this Murayama species was named in 1937, it is presumed that these "paratypes" are actually metatypes that were compared by Murayama to his type series. Murayama told me in 1955 that virtually all of his Manchurian collections had been destroyed during World War II. Consequently, the above "paratypes" are probably the only known existing specimens of *modestus* that are reasonably authentic. These "paratypes" were compared directly to my homotypes of *H. spessivtsevi* Eggers and were found to be normal, average specimens of this Eggers species. For this reason, the name *modestus* is placed in synonymy under the senior name, as indicated above.

Ips stebbingi Strohmeyer

Ips stebbingi Strohmeyer, 1908, Entomologischen Wochenblatt 25:69 (Syntypes, male, female; Kulu, Himalaya occidentalis; Strohmeyer Collection, Eberswald, Forest Research Institute, Dehra Dun, etc.)

Ips schmutzenhoferi Holzschuh, 1988, Entomologica Basiliensia 12:481–485 (Holotype, male; West-Bhutan, Chamgang, 3000 m; Naturhistorisches Museum Wien). *New synonymy*

I examined two syntypes of *Ips stebbingi* Strohmeyer in the Forest Research Institute Collection, Dehra Dun, as well as approximately 2,000 other specimens of this species from Pakistan, Nepal, Bhutan, and India (Kashmir, Punjab, Uttar Pradesh) from species of *Abies*, *Cedrus*, *Picea*, and *Pinus griffithii*. I am unable to distinguish my specimens that were compared to the Strohmeyer syntypes from two paratypes of *I. schmutzenhofer* Holzschuh or from a series taken in 1980 in Bhutan from *Picea spinulosa* by P. Singh. It is apparent from the description of *I. schmutzenhoferi* that specimens cited as *I. stebbingi* were actually of *I. longifolia*, a distinct, but related, species. In view of the above, *I. schmutzenhoferi* is here placed in synonymy, as indicated above.

Phloeosinus rudis Blandford

Phloeosinus rudis Blandford, 1894. Entomological Society of London. Transactions 1894:73 (Syntypes; Kashiwage and Kolbe, Japan; British Museum [Natural History])

Phloeosinus shotoensis Murayama, 1955. Yamaguti University Faculty of Agriculture. Bulletin 6:88 (Holotype, male; Japan: Omude, Shodojima, Kagawa pref.; U.S. National Museum). *New synonymy*

The type series of *Phloeosinus shotoensis* Murayama consisted of one male and six females from the type locality and seven females from other named localities. Murayama clearly states that the male is the type. All 13 specimens in the type series were compared to my homotypes of *P. rudis* Blandford. The Murayama specimens fall well within the range of variability of *rudis*. Because it is obvious that only one species is represented by these specimens, the name *shotoensis* is placed in synonymy as indicated above.

Polygraphus kaimochi (Nobuchi)

Nipponopolygraphus kaimochi Nobuchi, 1981, Kontyu 49:13 (Holotype, female; Shionomisaaka, Wakayama; Nobuchi Collection, Ibaraki)

Polygraphus querci Wood, 1988, Great Basin Naturalist 48:195 (Holotype, female; Mehalkhali [Burma?]; Forest Research Institute, Dehra Dun). *New synonymy*

The female holotype and two paratypes of *Nipponopolygraphus kaimochi* Nobuchi were compared directly to one another and to the type series of *Polygraphus querci* Wood by me and were found to represent only one species. The junior name, *querci*, is placed in synonymy as indicated above.

Polygraphus proximus Blandford

Polygraphus proximus Blandford, 1894, Entomological Society of London. Transactions 1894:75 (Syntypes, 2; Sapporo, Japan; British Museum [Natural History])

Polygraphus magnus Murayama, 1956, Yamaguti University Faculty of Agriculture. Bulletin 7:279, 282 (Holotype, female; Nishimata, Aki County, Kochi pref., Japan; U.S National Museum). *New synonymy*

The unique female holotype of *Polygraphus magnus* Murayama was examined and compared to my series of *P. proximus* Blandford that had been identified by Kurenzov, Nobuchi, and Pfeffer. A series of this species received from Murayama had been identified as *P. oblongus* Blandford and is presumed to be incorrectly placed by him. The *magnus* holotype is 3.2 mm in length (exclusive of the head), which is substantially smaller than stated in the original description. The pronotum of this specimen is contaminated by host resin, thereby giving both the stout bristles and scales the false impression that they are all scalelike. In reality, these setae are precisely as in normal specimens of *proximus*. In addition, the size falls well within the upper limits of size for *proximus*. The *magnus* holotype obviously is a normal, large female of *proximus*. For this reason, the Murayama name is placed in synonymy as indicated above.

Scolytogenes braderi (Browne)

Cryphalomorphus braderi Browne, 1965, Zoologische Mededelingen 40:191 (Holotype; Ivory Coast: Adiopodoume; Leiden Museum)

Cryphalomorphus orientalis Schedl, 1971, Opuscula Entomologica 119:11 (Holotype; Ghana, Bekwai; Naturhistorisches Museum Wien). *New synonymy*

The holotype of *Cryphalomorphus orientalis* Schedl, cited above, was compared directly by Schedl to the holotype of *Cryphalomorphus braderi* Browne, cited above, and (as indicated in a note in his collection) he concluded that only one species was represented. I examined the Schedl holotype and compared it to specimens identified by Schedl as *braderi* Browne and reached the same conclusion. In view of this, the name *orientalis* is here placed in synonymy as indicated above.

Scolytoplatypus parvus Sampson

Scolytoplatypus parvus Sampson, 1921, Annals and Magazine of Natural History (9)7:36 (Holotype, male; Sarawak, Mt. Matang; British Museum [Natural History])

Scolytoplatypus ruficauda Eggers, 1939, Arkiv for Zoologi 31A(4):36 (Holotype, female; Kambaiti, Nordost-Birma, 7000 ft.; Stockholm Museum). *New synonymy*

Four specimens of *Scolytoplatypus parvus* Sampson that were compared to the holotype by Browne were compared directly by me to nine specimens in the Forest Research Institute, Dehra Dun, that had been identified by Eggers as his S. *ruficauda*. They all represent the same species. Assuming that Eggers correctly identified his species, the name s. *ruficauda* must be placed in synonymy under the senior name S. *parvus*, as indicated above.

Sphaerotrypes querci Stebbing

Sphaerotrypes querci Stebbing, 1908, Indian Forest Memoirs, series 5, 1(1):5 (Syntypes, sex?; India, N-W Himalaya, Kumaun; Forest Research Institute, Dehra Dun, lost)

Chramesus globulus Stebbing, 1909, Indian Forest Memoirs, Forest Zoology series 1(2):21 (Holotype, Kathian, Chakrata, U.P., India; Forest Research Institute, Dehra Dun). Preoccupied

Sphaerotrypes tectus Beeson, 1921, Indian Forester 47:514 (Holotype, sex?; Kathian, Chakrata, U.P., India; Forest Research Institute, Dehra Dun, automatic). *New synonymy*

The series of *Sphaerotrypes querci* Stebbing in the Forest Research Institute, Dehra Dun, collected by Stebbing and others, does not include original specimens. However, Stebbing's identification, description, and notes clearly indicate that this name was correctly applied to his series. This material was examined and compared directly to the holotype of *Chramesus globulus* Stebbing by me. Both sets of specimens clearly represent the same species. Beeson recognized that the name *S. globosus* was preoccupied by Blandford and proposed the replacement name *S. tectus* for Stebbing's species. The senior synonym, *S. querci* Stebbing, has priority and is used to designate this species, as indicated above.

Sueus niisimai (Eggers)

Hyorrhynchus niisimai Eggers, 1926, Entomologische Blätter 22:133 (Holotype, female; Japan: Urakawa [Hokodate]; U.S. National Museum)

Sphaerotrypes controversae Murayama, 1950, Insecta Matsumurana 17:62 (Lectotype, female; Daidominami-yama, Kochi pref., Shikoku, Japan; U.S. National Museum, present designation). *New synonymy*

Murayama named *Sphaerotrypes controversae* from six female specimens mounted on two pins. Although he refers to a type, a holotype was not marked or labeled by Murayama. The two specimens mounted on separate points on one pin are covered by glue and are recognized with difficulty. On the other pin, the third specimen from the top (or the second one up from the bottom) is in the best condition and is here designated as the lectotype of *controversae*. These specimens were compared directly to my homotypes and other series of *Sueus niisimai* in my collection and are identical in all respects. Because only one species is represented, the name *controversae* is placed in synonymy under the senior name as indicated above.

Tomicus brevipilosus (Eggers)

Blastophagus brevipilosus Eggers, 1929, Entomologische Blätter 25:103 (Syntypes, 2; [Fukien] China; Eggers Collection)

Blastophagus khasianus Murayama 1959, Brooklyn Entomological Society, Bulletin 54:75 (Holotype; Shillong, Assam, India; U.S. National Museum). *New synonymy*

Blastophagus multisetosus Murayama, 1963, Studies in the scolytid fauna of the northern half of the Far East, Shukosh Press, Fukuoka, p. 37 (Holotype, female; Mt. Manza, Gunma pref., Japan; U.S. National Museum). *New synonymy*

The female holotype of *Blastophagus multisetosus* Murayama, my topotypic homotypes of *B. khasianus* Murayama, and my homotypes of *B. brevipilosus* Eggers were all compared directly to one another. Although the Assam specimens are somewhat larger, all share the very short interstrial setae and are here placed in the same species. This species is very closely allied to *piniperda* (Linnaeus) and is distinguished with some difficulty from that species by the setal characters. It is currently placed in the genus *Tomicus* under the senior name *brevipilosus* as indicated above.

NEW INTRODUCTIONS

Hylastes opacus Erichson

Hylastes opacus Erichson, 1836, Archiv für Naturgeschichte 2(1):51 (Syntypes; presumably Germany; Berlin Museum)

A series of *Hylastes opacus* Erichson was collected near the eastern tip of Long Island on Fisher's Island, Suffolk Co., New York, USA, 23 May 1989, from an *Ips* pheromone trap, by T. W. Phillips. Circumstances of the collection suggest that this species has established a breeding population at that site. This species is common throughout the pine belts of Europe and northern Asia and it has become established in pine plantations in South Africa. While it breeds primarily in the roots and stumps of pine (*Pinus* spp.) and spruce (*Picea* spp.), it is known as an economic pest of small seedlings of these trees.

Phloeosinus armatus Reitter

Phloeosinus armatus Reitter, 1887, Wiener Entomologische Zeitung 6:192 (Holotype, male; Syrien; Naturhistorisches Museum Wien)

This species was recently found to be established in Los Angeles Co., California, USA, in a broad area in sufficient numbers to cause economic losses in *Cupressus* spp. It was previously known from Cyprus, Syria, and Israel, where it is an important pest of *Cupressus* spp.

NEW SPECIES

Cyclorhipidion subagnatum, n. sp.

Schedl (1957:100) cited *Xyleborus subagnatus* Eggers, nomen nudum. He later (Schedl 1961:94) expressed the opinion that

X. subagnatus Eggers, from the Philippine Islands, was actually *X. parvus* Lea (of Australia), and he published a complete description of the Philippine series in that article under the name of *X. parvus*. Later, he (Schedl 1964:314) saw the type of *X. parvus*, recognized the differences in the two taxa, and presented the new name *S. subagnatus* Schedl for the Philippine series. He then (Schedl 1979:239) designated a "lectotype" for *X. subagnatus* Schedl.

Because *X. subagnatus* Eggers was never validated, Schedl's presentation of a new name for it did not meet the requirements of the Code of Nomenclature even though a description exists for the taxon. This taxon has been transferred to the genus *Cyclorhipidion*, where it is treated here.

Cyclorhipidion subagnatum is presented here as a species new to science. The validating description is published in Schedl (1961:94–95) under the misidentified name *Xyleborus parvus* Lea. The female holotype is the specimen labeled as the "lectotype" of *Xyleborus subagnatus* Schedl in the Naturhistorisches Museum Wien. The type locality is Mt. Irid, Luzon, Philippine Islands. Other specimens in this Schedl series from this locality in the Wien Museum are paratypes.

Dendrotrupes zealandicus, n. sp.

This species is distinguished from *costiceps* Broun, the only other named species in this genus, by the smaller body size, by the less strongly impressed male frons that lacks a median epistomal denticle, and by the more evenly rounded elytral declivity.

MALE.—Length 1.5–1.7 mm, 2.7 times as long as wide; color brown, elytra mostly light brown.

Frons broadly, moderately concave from epistoma to slightly above eyes, deepest at its center, upper area subrugulose and punctured, lower third more nearly shining and subaciculate; lateral margins subacute only near antennal insertions, rounded above; a fine median carina from center of concavity to epistomal margin, usually higher on lower third, without a denticle near epistoma (as seen in *costiceps*). Vestiture hairlike, rather sparse and inconspicuous; not conspicuously longer and more abundant on margins as in *costiceps*.

Pronotum 0.9 times as long as wide; similar to *costiceps* except punctures more sharply, more strongly impressed, hairlike setae shorter, less conspicuous.

Elytra 1.7 times as long as wide, outline similar to *costiceps*; striae 1 slightly, others not impressed, punctures rather small, round, deep; interstriae as wide as striae, smooth, shining, punctures minute, confused, moderately abundant. Declivity gradual, not steep, evenly, rather narrowly convex; sculpture as on disc except interstriae 1–3 each with a row of about six minute granules; vestiture much less abundant than in *costiceps*, interstrial rows of erect setae rather slender, each about as long as distance between rows, ground cover recumbent, each seta about half as long as erect setae.

FEMALE.—Similar to male except frons convex, carina less conspicuous.

TYPE MATERIAL.—The male holotype, female allotype, and two male paratypes are from Rotorua, New Zealand, Hopk. US 3726-U, C. L. Massey. The holotype, allotype, and paratypes are in my collection.

Polygraphus thitsi, n. sp.

The name *Spongocerus thitsi* Beeson (1941:387), nomen nudum, was used by Beeson without a description or designation of type material, either in the original publication or on specimens in his collection. Browne (1970:550) recognized this deficiency and attempted to correct the problem by designating a Beeson specimen as "lectotype" and presenting a description of it. However, in order for a lectotype to become a primary type it must be validly designated (Code of Nomenclature, 1985, Article 74a). In the present case, because *Spongocerus thitsi* Beeson was a nomen nudum, a type series did not exist; and because there were no syntypes, a lectotype could be not be validly designated. Therefore, regardless of the action by Browne (1970:550), Beeson's nomen nudum remained invalid. The name *Spongotarsus* is currently a synonym of *Polygraphus*; consequently, the species cited as *thitsi* is here transferred to that genus (Wood 1986:56).

For the purpose of validating this name, *Polygraphus thitsi* is presented here as new to science. It is allied to *P. kaimochii* Nobuchi, from Burma, but it is distinguished by the much larger size (4.7–5.8 mm), by the completely divided eye, by the larger pronotal punctures, by the more slender elytral scales, and by the host.

Browne (1970:550) presents a full description of *P. thitsi*. Browne's invalid "lectotype" is here designated as the female holotype of *P. thitsi*. Except that the type locality, Namma Reserve (Burma) is incorrectly spelled, Browne's data are correct; it is in the British Museum (Natural History). The male allotype has the lower half of the frons shallowly, almost concavely impressed on the median third; it bears data identical to the holotype and is in my collection. One female paratype in my collection and 47 paratypes of both sexes in the Forest Research Institute bear data identical with that of the holotype.

Triotemnus pilicornis, n. sp.

This species is distinguished from *zeylanicus* Wood, below, by the slightly larger size, by the lighter color, by the coarser pronotal punctures, by the very large, median horn on the male vertex, and by the very small mandibular spines in the male.

MALE.—Length 1.5–2.2 mm (female slightly smaller); 2.5 times as long as wide; color brown.

Frons strongly, transversely excavated, feebly if at all concave between eyes; a very large, dorsoventrally flattened, median spine on vertex (this spine often more than twice as long as scape); surface smooth, shining, glabrous, dorsal surface of spine strongly pubescent, these setae very long.

Pronotum very slightly longer than wide, subquadrate; surface smooth, shining, punctures coarse, deep. Vestiture sparse, rather short, very long and conspicuous on lateral and anterior margins.

Elytra similar to *zeylanicus* except punctures slightly smaller; setae more slender, declivity more broadly convex.

FEMALE.—Similar to male except: frons weakly, transversely impressed (stronger than female *zeylanicus*), moderately punctured; without spines on vertex or mandibles.

TYPE MATERIAL.—The male holotype, female allotype, and six paratypes were taken at Chikalda, Malgahat, C.P., India, 16-X-1936, R.R.D. 106, R.C.R. 181, Cage 660, from *Euphorbia* sp. by N. C. Chatterjee; all are mounted on two pins. The holotype is the uppermost specimen and the allotype is the third specimen down on the same pin. The holotype, allotype, and paratypes are in my collection. More than 480 non-type specimens were examined at the Forest Research Institute, Dehra Dun, from the states of Karnataka, Madhya Pradesh, and Maharashtra from *Euphorbia* spp.

Xyleborus magnificus, n. sp.

This species is distinguished from *X. spathipennis* Eichhoff by its larger body size, by the much more broadly, less steeply convex elytral declivity, by the much less strongly impressed elytral striae, and by other details described below. It is a much stouter species than *X. princeps* Blandford. In a series of *spathipennis* from the same locality and date, the strial punctures on the disc are mostly confluent; in *magnificus* they are mostly separate.

FEMALE.—Length 5.6 mm (paratypes 5.5–5.7 mm), 2.3 times as long as wide; color very dark brown.

Frons about as in *spathipennis*.

Pronotum similar to *spathipennis* except: anterior margin less strongly produced (straighter), serrations less well developed; discal area smoother, punctures smaller.

Elytra similar to *spathipennis* except: form slightly stouter, posterior margin more broadly rounded; profile of upper declivity more strongly, less evenly arched; striae much less strongly impressed on disc, not at all impressed on declivity; interstriae much more broadly convex on disc, flat on declivity, punctures smaller, more numerous, more obscure and almost never replaced by minute granules on declivity; declivital interstriae 2 and 4 never with setae (a few short setae present in *spathipennis*).

TYPE MATERIAL.—The female holotype and five female paratypes are labeled: Junin [presumably Peru], 01-IX-79, S. Poncor, EESC, 5-80. The holotype and paratypes are in my collection.

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NOMENCLATURAL CHANGES IN SCOLYTIDAE AND PLATYPODIDAE (COLEOPTERA)

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ABSTRACT.—New synonymy in Scolytidae includes *Cryphalus piceae* (Ratzeburg, 1837) (=*Cryphalus subdepressus* Eggers, 1940), *Gnathotrupes longiusculus* (Schedl, 1951) (=*Gnathotrupes ciliatus* Schedl, 1975), *Hypothenemus eruditus* Westwood (=*Stephanoderes communis* Schaufuss, 1891). In Platypodidae the new name *Platypus abruptifer* is proposed as a replacement for the junior homonym *Platypus abruptus* Browne, 1986; type-species designations are proposed for the genus-group names *Scutopygus* Nunberg, 1966, *Pygodolius* Nunberg, 1966, *Mixopygus* Nunberg, 1966, *Mesopygus* Nunberg, 1966, *Asetus* Nunberg, 1958, *Stenoplatypus* Strohmeyer, 1914, *Platypinus* Schedl, 1939, *Platyscapus* Schedl, 1939, *Treptoplatypus* Schedl, 1939, *Tesseroplatypus* Schedl, 1935; previously unpublished specific synonymy is presented for *Crossotarsus externedentatus* (Fairmaire, 1849) (=*Diapus talurae* Stebbing, 1906), *Crossotarsus terminatus* Chapuis, 1865 (=*Crossotarsus nicobaricus* Beeson, 1937), *Platypus abditus* Schedl, 1936 (=*Platypus transitus* Schedl, 1978), *Platypus rugosifrons* Schedl, 1933 (=*Platypus pretiosus* Schedl, 1961), *Platypus tiriosensis* Reichardt, 1965 (=*Platypus schedli* Wood, 1966), *Treptoplatypus multiporus* Schedl, 1968 (=*Platypus fastuosus* Schedl, 1969).

Key words: Scolytidae, Platypodidae, Coleoptera, nomenclature.

The following pages record items affecting nomenclature in Scolytidae and Platypodidae that are presented here in order to make the changes available for the world catalog now in preparation for these families. Included are three cases of new specific synonymy in Scolytidae. In Platypodidae are (a) one new replacement name for a junior homonym, (b) 10 type-species designations for genus-group names, and (c) six new cases of specific synonymy.

NEW SYNONYMY IN SCOLYTIDAE

Cryphalus piceae (Ratzeburg)

Bostrichus piceae Ratzeburg, 1837, Die Forst-insekten, Käfer 1:163 (Syntypes; Oberschlesien un Baiern; Institut für Pflanzenschutz, Eberswalde)

Cryphalus subdepressus Eggers, 1940, Centralblatt für Gesamte Forstwesen 66:37 (Holotype; Kleinasien [Avancik in northern Turkey]; Eggers Collection, in Naturhistorisches Museum Wien). *New synonymy*

A Schedl note in his collection indicates that *Cryphalus subdepressus* Eggers (from northern Turkey), cited above, is synonymous with *C. kurenzovi* Stark (=*C. punctulatus* Eggers) from the Far East of USSR, and with *C. piceae* as identified by Reitter. In the absence of known specimens of *kurenzovi* west of Ussuri and of the occurrence of *piceae* Ratzeburg, cited above, throughout Europe and northern Asia, it appears prudent to follow Reitter and recognize the Turkish population as *piceae*. For this reason, the name *subdepressus* is placed in synonymy as indicated above.

Gnathotrupes longiusculus (Schedl)

Gnathotrichus longiusculus Schedl, 1951, Dusenia 2:121 (Holotype, male; Tierra del Fuego, Via Monte; Eggers Collection, Naturhistorisches Museum Wien)

Gnathotrupes ciliatus Schedl, 1975, Studies on the Neotropical Fauna 10:4 (Holotype, female; Argentina, Nahuel Huapi National Park; Naturhistorisches Museum Wien). *New synonymy*

The male holotype of *Gnathotrichus longiusculus* Schedl, cited above, and the female holotype of *Gnathotrupes ciliatus* Schedl, cited above, were compared directly to one another and to other males and females of this species in the Schedl Collection and in my collection. Because distinguishing characters that might be used to separate species are absent, it is apparent that only one species is represented by this material. The name *ciliatus* is placed in synonymy in the genus *Gnathotrupes* as indicated above.

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Hypothenemus eruditus Westwood

Hypothenemus eruditus Westwood, 1836, Entomological Society of London, Transactions 1:34 (Syntypes, female; England; some in British Museum [Natural History], London)

Stephanoderes communis Schaufuss, 1891, Tijdschrift voor Entomologie 34:11 (Holotype, female; Madagascar; Schedl Collection in Naturhistorisches Museum Wien). *New synonymy*

The female holotype of *Stephanoderes communis* Schaufuss, cited above, has the head missing and most of the body scales have been rubbed off, but there is no doubt whatever that it represents a normal female of *Hypothenemus eruditus* Westwood. The holotype of *communis* was examined by me and compared directly to my homotypes of *eruditus*. This is the most common species of Scolytidae in the world, although it is often recognized with difficulty, as in this case. The new synonymy is indicated above.

NEW NAME IN PLATYPODIDAE

Platypus abruptifer, n. n.

Platypus abruptus Browne, 1986, Kontyo 54:337 (Holotype, male; New Guinea: Adi Island to Nagoya [Japan], imported; British Museum [Natural History], London), preoccupied by Sampson 1923

The name *Platypus abruptus* Browne, cited above, is a junior homonym and must be replaced. The new name, *abruptifer*, is proposed as a replacement as indicated above.

GENERIC CHANGES IN PLATYPODIDAE

Doliopygus Schedl

Doliopygus Schedl, 1939, International Congress of Entomology, Proceedings 7:402-403, type-species: *Crossotarsus bohemani* Chapuis, designated by Schedl 1972

Scutopygus Nunberg, 1966, Revue de Zoologie et de Botanique Africaines 74:187-188, type-species: *Crossotarsus rapax* Sampson, present designation. *New synonymy*

Pygodolius Nunberg, 1966, Revue de Zoologie et de Botanique Africaines 74:188-189, type-species: *Crossotarsus regrandis* Sampson, present designation. *New synonymy*

Mixopygus Nunberg, 1966, Revue de Zoologie et de Botanique Africaines 74:188, type-species: *Crossotarsus conradti* Strohmeyer, present designation. *New synonymy*

Mesopygus Nunberg, 1966, Revue de Zoologie et de Botanique Africaines 74:187-188, type-species: *Crossotarsus ukerewensis* Schedl, present designation. *New synonymy*

For the genus *Doliopygus* Schedl, Nunberg named the four subgenera cited above, without designating a type-species for them. To remove this ambiguity from these names, a type-species is designated above for each of them. Because *Doliopygus* contains only 142 species and the diversity within the genus is only moderate, it is felt that subgenera in this genus are not needed at the present time. These Nunberg names are regarded as synonyms of *Doliopygus*, as indicated above.

Periommatus Chapuis

Periommatus Chapuis, 1865, Monographie des Platypides, p. 42, 316, type-species: *Periommatus longicollis* Chapuis, monobasic

Asetus Nunberg, 1958, Acta Zoologica Cracoviensia 2:10, type-species: *Periommatus severini* Strohmeyer, present designation, synonymy by Schedl 1972

The name *Asetus* Nunberg, cited above, was established and then placed in synonymy under *Periommatus* as indicated. Even though it is an essentially unused name, in order to remove ambiguity from citations of it, a type-species must be designated. This designation is given above.

Platypus Herbst

Platypus Herbst, 1793, Natursystem aller bekannten . . . Insekten, Der Käfer 5:128, type-species: *Bostrichus cylindrus* Fabricius, monobasic

Stenoplatypus Strohmeyer, 1914, Genera Insectorum, Fasc. 163:35, type-species: *Crossotarsus spinulosus* Strohmeyer, present designation, synonymy by Schedl 1939

Platypinus Schedl, 1939, International Congress of Entomology, Proceedings 7:397, type-species: *Platypus curtus* Chapuis, present designation, synonymy by Wood 1979

Platyscapus Schedl, 1939, International Congress of Entomology, Proceedings 7:397, type-species: *Platypus carinulatus* Chapuis, present designation, preoccupied by Huistache 1921, renamed *Platyscapulus* Schedl 1957, synonymy by Browne 1962

The genus-group names *Stenoplatypus* Strohmeyer, *Platypinus* Schedl, and *Platyscapus* Schedl (=*Platyscapulus* Schedl), cited above, were named without the designation of a type-species. To remove this deficiency and the consequent ambiguity associated with them, type-species are designated as indicated above. All three names are junior synonyms of *Platypus* Herbst.

Tesserocerus Saunders

Tesserocerus Saunders, 1836, Entomological Society of London,Transactions 1:155, type-species: *Platypus* (*Tesserocerus*) *insignis* Saunders, monobasic

Tesseroplatypus Schedl, 1935, Entomologische Nachrichten 9:149, type-species: *Tesseroplatypus ursus* Schedl =*Tesserocerus insignis* Saunders, present designation, synonymy by Schedl 1972

The genus-group name *Tesseroplatypus* Schedl, cited above, was proposed without the designation of a type-species. To remove this deficiency, a type-species is designated as indicated above. The name was placed in synonymy several years ago, as indicated.

Treptoplatypus Schedl

Treptoplatypus Schedl, 1939, International Congress of Entomology, Proceedings 7:401, type-species: *Crossotarsus trepanatus* Chapuis, present designation

The generic name *Treptoplatypus* Schedl, cited above, was named without the designation of a type-species. To remove this deficiency, a type-species is designated above, as indicated.

NEW SYNONYMY IN PLATYPODIDAE

Crossotarsus externedentatus (Fairmaire)

Platypus externedentatus Fairmaire, 1849, Revue et Magasin de Zoologie Pure et Appliquée, ser. 2, 2:78 (Holotype, male; Taiti; Museum National d'Histoire Naturelle, Paris)

Diapus talurae Stebbing, 1906, Departmental notes on insects that affect forestry (Calcutta), No. 3, p. 418 (Syntypes: India: Madras Presidency, N. Coimbatore Forests; Forest Research Institute, Dehra Dun. *New synonymy*

The species *Diapus talurae* Stebbing, cited above, was described as occurring throughout India in economically significant numbers. Reports from 1906 through 1908 repeat the original report. It was last mentioned in original literature in Stebbing 1914 (Indian Forest Insects, p. 626), where it was transferred to the genus *Platypus*.There are no specimens under this name or host (*Shorea talura*) in the Forest Research Institute, Dehra Dun, nor is the type locality represented on an Indian platypodid. The Stebbing 1914 illustration is of a *Crossotarsus* species, probably *externedentatus* (=*saundersi*). Because so many of Stebbing's Platypodidae in the FRI Collection are misidentifications of this species, *talurae* is placed in synonymy under *externedentatus*, as indicated above, based on the Stebbing illustration in the absence of other evidence. The fact that it was said to be a common, economic species supports this placement.

Crossotarsus terminatus Chapuis

Crossotarsus terminatus Chapuis, 1865, Monographie des Platypides, p. 83 (Holotype, male; Singapour; British Museum [Natural History], London)

Crossotarsus nicobaricus Beeson, 1937, Indian Forest Records, Entomology 3:86 (Syntypes: Nicobars: Car Nicobar; Forest Research Institute, Dehra Dun). *New synonymy*

The male holotype and seven paratypes of *Crossotarsus nicobaricus* Beeson, cited above, were compared by me directly to the Beeson series of *C. venustus* Chapuis (=*C. terminatus* Chapuis), cited above, and two of these to my series of *C. terminatus*. In the absence of distinguishing characters, all were considered to represent the same species. For this reason the name *nicobaricus* is placed in synonymy, as indicated above.

Platypus abditus Schedl

Platypus abditus Schedl, 1936, Revue Française d'Entomologie 2:246 (Holotype, male; Naturhistorisches Museum Wien)

Platypus transitus Schedl, 1978, Entomologische Abhandlungen Staatliches Museum für Tierkunde in Dresden 41:309 (Holotype, male; Brasilien, Linhares, E. Santo; Naturhistorisches Museum Wien). *New synonymy*

The male holotypes, cited above, of *Platypus abditus* Schedl and of *P. transitus* Schedl were compared by me directly to one another and to other representatives of this species. Because distinguishing characters could not be found, the junior name, *transitus*, is placed in synonymy, as indicated above.

Platypus rugosifrons Schedl

Platypus rugosifrons Schedl, 1933, Revista de Entomologia, São Paulo 3:173 (Holotype, male; Brazil, S. Paulo, Alto da Serra; Naturhistorisches Museum Wien)

Platypus pretiosus Schedl, 1961, Pan-Pacific Entomologist 37:233 (Holotype, male; Venezuela, Mt. Duida; California Academy of Science, San Francisco). *New synonymy*

The male holotype of *Platypus rugosifrons* Schedl, cited above, and the male paratype of *P. pretiosus* Schedl in the Schedl Collection were compared directly to one another and to my homotypes of this species. Because only one species appears to be represented by this material, the junior name, *pretiosus*, is placed in synonymy as indicated above.

Platypus tiriosensis Reichardt

Platypus tiriosensis Reichardt, 1965, Papeis Avulsos do Departamento de Zoologia, Secretaria de Agricultura, São Paulo 17:53 (Holotype, male; Brasil, Estado de Para, Tirios (Alto rio Paru d'Oeste; Departamento de Zoologia, Secretaria da Agricultura, São Paulo)

Platypus schedli Wood, 1966, Great Basin Naturalist 26:51 (Holotype, male; Manaka, British Guiana; British Museum [Natural History], London). *New synonymy*

Although direct comparisons of holotypes were not made, it is apparent from published illustrations and from my examination of the Schedl male of *Platypus tiriosensis* Reichardt, cited above, and of the *P. schedli* type series, that these names are synonyms. Both Reichardt and I sent specimens of this species to Schedl in 1964 for comparison to related species. We both received encouragement from him to name the species, although subsequent events clearly indicated that he was fully aware we were both working with the same species. The name *schedli* is placed in synonymy as indicated above.

Treptoplatypus multiporus Schedl

Treptoplatypus multiporus Schedl, 1968, Pacific Insects 10:270 (Holotype, female; Okapa (kasa), E. Highlands District [New Guinea]; CSIRO, Canberra)

Platypus fastuosus Schedl, 1969, Linnean Society of New South Wales, Proceedings 94:226 (Holotype, male; New Guinea: Marafunga, 2800 m; CSIRO, Canberra). *New synonymy*

Schedl named *Treptoplatypus multiporus*, cited above, from the female and *Platypus fastuosus*, cited above, from the male. Subsequent collecting has demonstrated that these names represent the opposite sexes of the same species. A note in his collection indicates that Schedl was aware of this problem. Both holotypes, as well as additional material, were examined. The junior name, *fastuosus*, is placed in synonymy as indicated above.

Received 3 March 1992
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Great Basin Naturalist 52(1), 1992, p. 93

BOOK REVIEW

Plant biology of the Basin and Range. C. B. Osmond, L. F. Pitelka, and G. M. Hidy. Springer-Verlag, Berlin, 1990. 375 pp. $69.50.

This intriguing volume will be of interest to many people for a variety of reasons. It was written to honor W. Dwight Billings, who began his distinguished career in what is now called physiological ecology at the University of Nevada at Reno. Although he moved to Duke University in 1952, his heart, and considerable research, remained in Nevada. Twenty-seven authors contributed the nine chapters of the book. While that is generally enough to make one move on to something else, in this case it would be a mistake. Although the book was not what I expected, I was pleasantly surprised. The chapters are very uneven and range from the broad and general to the narrow and highly technical. The contributors are first rate and the chapters well written. I suggest that the reader browse, first reading whatever appeals and then perhaps returning to some of the other areas.

The strangest chapter in the book is the first one. It is a nice introduction but in spite of its title is neither about anthropology or botany. The dynamics of climate in the Basin is the subject of the next chapter. Brief but interesting, it is clearly written for the nonclimatologist. The heart of the book is the 40-page chapter by Billings himself on mountain forests of North America. It clearly extends beyond the Great Basin but should be required reading of every student of plant ecology. Here is the master giving us the distilled wisdom of decades of research and thinking. We then move on to high-elevation forests in an excellent chapter on the difficult problems imposed on living things by the harsh conditions associated with altitude. There are high mountains not only surrounding but running through the Basin in a north-south direction. Edaphic factors and their influence on water and nutrient availability and subsequent plant distribution are next considered. There are islands of very disjunct soils throughout the Basin.

Chapter 6 examines what most of us think of in the Great Basin—the lowland plants. The emphasis is on ecophysiology, and broad patterns are the theme. Martyn Caldwell and his co-workers have spent many years studying the root systems of desert plants. This summary of their work is well worth careful study. However, I was surprised to find only a cursory mention of the role of mycorrhizae. Chapter 8 deals with isotopes and vegetation changes. That sounds narrow and well focused but the chapter was not. It is an overview of the potential use of carbon isotopes in physiological ecology. The last chapter deals briefly with climatic change in the Great Basin. The past has been very dynamic and exciting. What may we expect in the future?

While I was disappointed by some of the things the title seemed to promise and did not deliver, I did like the book and recommend it highly. As in many books with contributed chapters, the lack of continuity or transition between chapters left an overall impression of a disjointed and uneven approach. In spite of this, we can be grateful for what was delivered: well-written text that was fascinating and stimulating in places, nice illustrations, good index. Physiological ecologists interested in the Great Basin should spend some time with this volume.

Bruce N. Smith
Department of Botany and Range Science
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INFORMATION FOR AUTHORS

The *Great Basin Naturalist* welcomes previously unpublished manuscripts pertaining to the biological natural history of western North America. Preference will be given to concise manuscripts of up to 12,000 words.

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RED BUTTE CANYON RESEARCH NATURAL AREA: HISTORY, FLORA, GEOLOGY, CLIMATE, AND ECOLOGY

James R. Ehleringer[1], Lois A. Arnow[1], Ted Arnow[2],
Irving B. McNulty[1], and Norman C. Negus[1]

Abstract.—Red Butte Canyon is a protected, near pristine canyon entering Salt Lake Valley, Utah. It contains a well-developed riparian zone and a perennial stream; hillside vegetation ranges from grasslands on the lower limits to Douglas-fir and aspen stands at the upper elevations. In this paper we describe the history of human impact, natural history aspects of climate, geology, and ecology, and faunal and floral information for key species in the canyon. The role and importance of Research Natural Areas is discussed, particularly with respect to the need to protect Red Butte Canyon—one of the few remaining undisturbed riparian ecosystems in the Intermountain West.

Key words: grassland, Intermountain West, oak-maple, plant adaptation, Red Butte Canyon, Research Natural Area, riparian ecology.

Red Butte Canyon, one of many canyons in the Wasatch Range of Utah, opens westward into Salt Lake Valley, immediately east of the University of Utah (Fig. 1). Like most canyons along the Wasatch Front, it is a grassland at the lowest elevations, is forested at its upper end, and has a perennial stream. What makes this canyon unusual is its history. The canyon was the watershed for Fort Douglas, the U.S. Army post built in 1862 that overlooked Salt Lake City. As a protected watershed, these lands were, for the most part, kept free from grazing, farming, and other human-impact activities. When the U.S. Army declared these lands surplus in 1969, the U.S. Forest Service assumed responsibility for the canyon. Since that time, Red Butte Canyon has been kept in its protected state and designated a Research Natural Area (RNA).

The Research Natural Area designation denotes an area that has been set aside because it contains unusual or unique features of substantial value to society. These might include unique geological features, endangered plant and animal species, or areas of particular value for scientific research as baseline bench marks of ecosystems that have been largely destroyed by human impact. In the case of Red Butte Canyon, the RNA designation was given because this canyon is one of the few remaining (if not the last) undisturbed watersheds in the Great Basin. The U.S. Forest Service report proposing that Red Butte Canyon be declared a Research Natural Area described the canyon as ". . . a living museum and biological library of a size that exists nowhere else in the Great Basin . . . an invaluable bench mark in ecological time." The Red Butte Canyon RNA is unique because it is a relatively undisturbed watershed adjacent to a major metropolitan area (Salt Lake Valley). To protect this valuable resource, access to the Red Butte Canyon RNA has been largely restricted to scientific investigators. One of the

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[2] Consulting geologist, 1064 E. Hillview Drive, Salt Lake City, Utah 84124

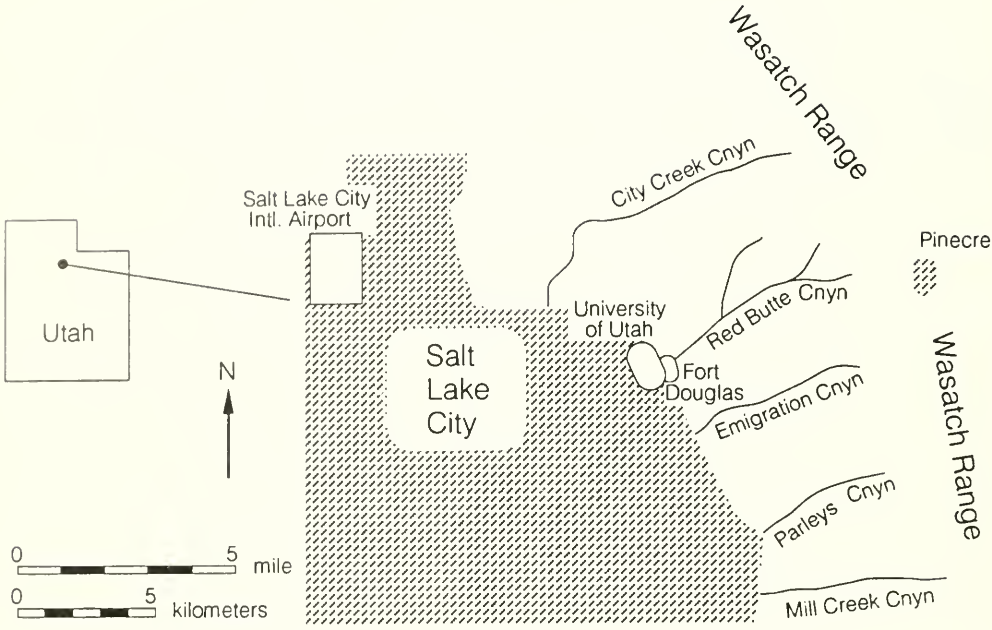
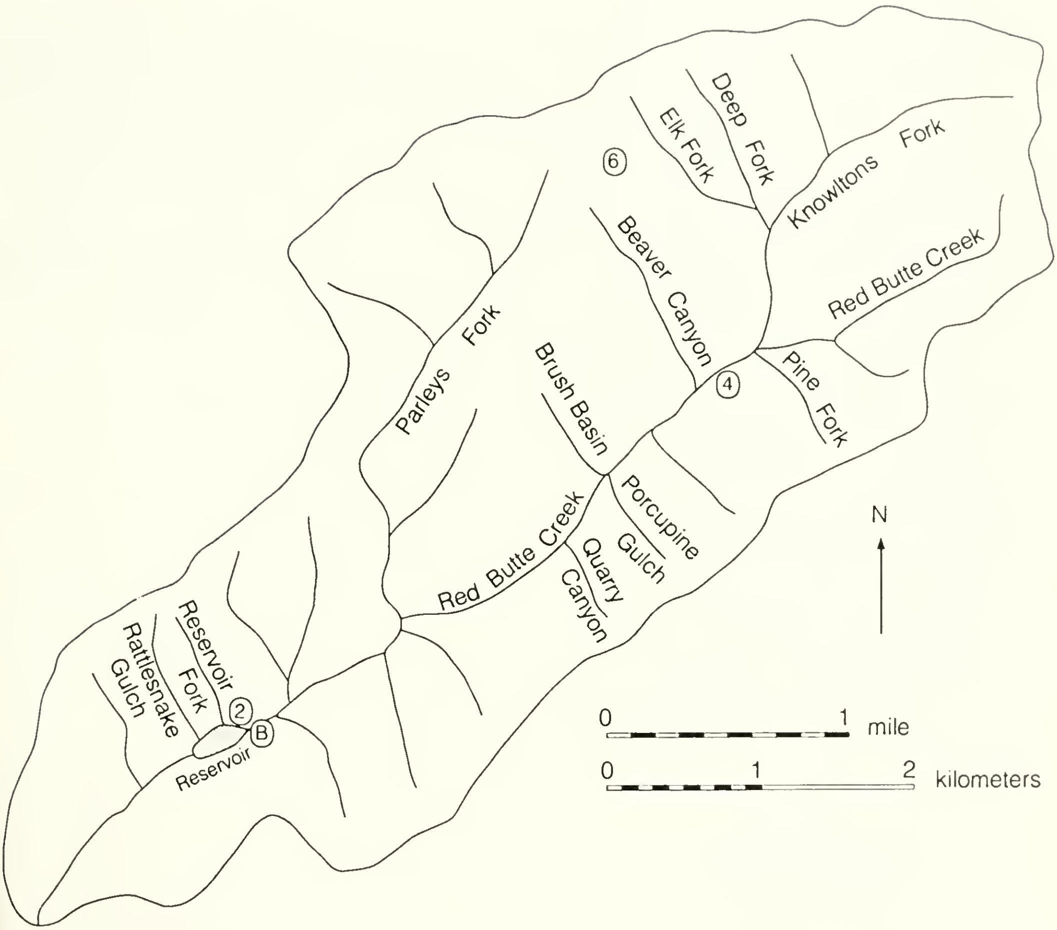


Fig. 1. Location of Red Butte Canyon and other sites referred to in text.

goals of the RNA Program is to protect and preserve a representative array of all significant natural ecosystems and their inherent processes as baseline areas. A second goal is to conduct research on ecological processes in these areas to learn more about the functioning of natural versus manipulated or disturbed ecosystems. Research activities in the Red Butte Canyon RNA are directed at both of these goals: understanding basic ecological processes (physiological adaptation, drought adaptation, nutrient cycling, etc.) and also the impact of humans on our canyons through both airborne (air pollution, acid rain, etc.) and land-related (grazing, human traffic, etc.) activities. The latter are conducted through comparison of Red Butte with other canyons along the Wasatch Range.

In size, Red Butte Canyon is relatively small compared with other drainages along the Wasatch Front. The drainage basin covers an area of approximately 20.8 km^2 (5140 acres) (Fig. 2). The drainage arises on the east from a minor divide between City Creek and Emigration canyons and drains to the west. The canyon has two main forks (Knowltons and Parleys) and many side canyons. Near the canyon base, a reservoir was constructed earlier this century to provide a more stable water supply to Fort Douglas. The diversity of slope and aspect combinations of the terrain contributes to a variety of biotic communities along an elevation gradient from about 1530 m (5020 ft) on the west end to more than 2510 m (8235 ft) at the crest.

The purpose of this paper is to provide a brief description of the history, flora, geology, climate, and ecology of this unusual and valuable resource. There is increasing interest in Red Butte Canyon, in part by scientific investigators because of its utility as a protected, undisturbed watershed, and in part by curious citizens from the nearby Salt Lake Valley. Yet, there has not been an overall reference available for those interested in general features of the canyon or past ecological studies within the canyon. Most of the information on Red Butte Canyon is scattered. With the closure of Fort Douglas in 1991, many of the historical records will become more difficult to access. It is hoped that the synthesis presented in this paper will provide the necessary background for those interested in the history and ecology of the Red Butte Canyon RNA. Irving McNulty first summarizes the history of the canyon, followed by Ted Arnow's description of geology and soils. James Ehleringer contributed the hydrology, climate, and plant ecology sections. The section on vascular flora was prepared by Lois Arnow, and Norman Negus wrote the mammalian and avian fauna sections.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2 kilometers

Fig. 2 Major drainages and weather and bench mark stations within the Red Butte Canyon Research Natural Area. B represents the location of the USGS Bench Mark station; circles numbers 2, 4, and 6 represent the locations of weather stations known as Red Butte #2, Red Butte #4, and Red Butte #6, respectively.

HISTORY

The history of Red Butte Canyon comes as bits and pieces from many sources, including Arrington and Alexander (1965), Hibbard (1980), and the Fort Douglas Army Engineers Office (1954), records of the Fort Douglas Museum, and discussions with C. G. Hibbard (Fort Douglas historian) and Harold Shore (Fort Douglas water master overseeing Red Butte Canyon). It is primarily a history of human impact on the utilization of natural resources provided by the canyon. Major resources were water from the stream and sandstone quarried for use in construction. Of minor importance were grazing and timber. In 1848, just one year after the arrival of the first pioneers in Salt Lake Valley, red sandstone was first quarried in the canyon to be used in construction in the building of Salt Lake City. It was the closest source of construction-quality sandstone and was quarried for almost 100 years. This mining had considerable impact on the plant and animal life in the lower portion of the canyon. The major use of Red Butte Creek water was by the U.S. Army at Fort Douglas, which was established at the mouth of the canyon in 1862. This utilization of water outside the canyon had little effect on the canyon itself, as U.S. Army administrators worked over many years to protect the watershed and water quality. In fact, protection has grown steadily since Fort Douglas was first established, and particularly since the canyon was acquired by the U.S. Forest Service in 1969 and declared to be a Research Natural Area.

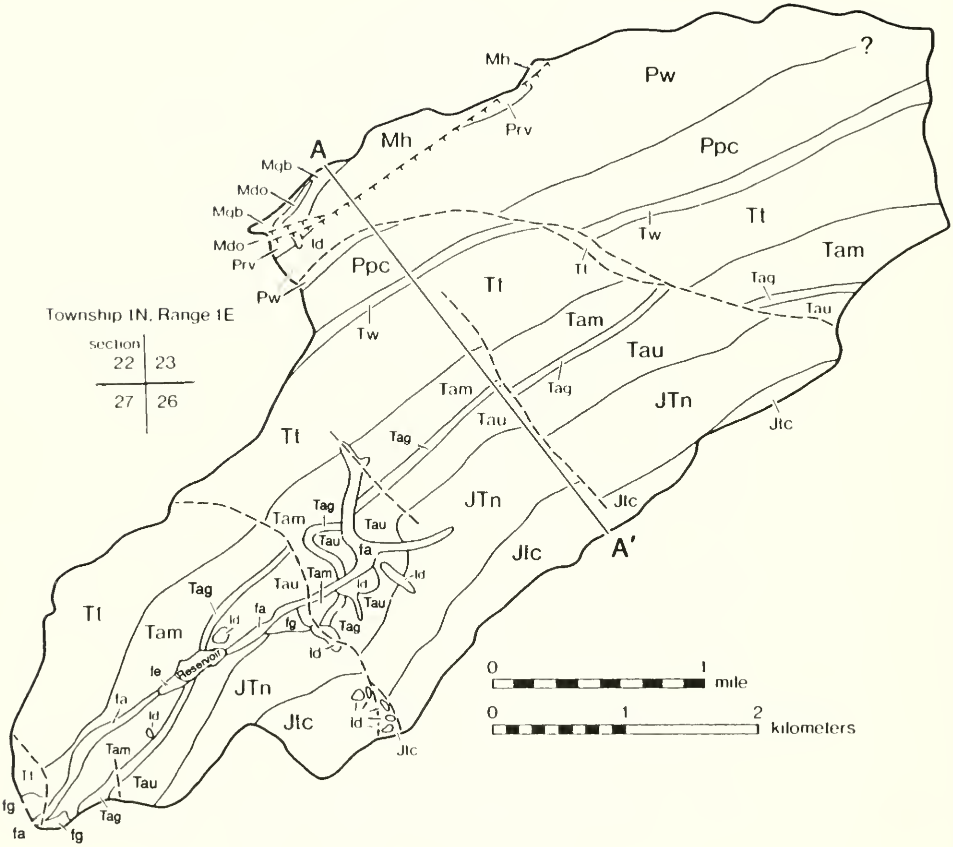
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Fig. 3 Geologic map of Red Butte Canyon Research Natural Area. See Table 1 for a description of abbreviations. Solid lines represent contacts between formations, dashed lines represent normal faults, and T-dashed lines represent the Black Mountain thrust fault. The transect A-A′ is shown in cross section in Figure 4. Adapted from Marsell and Threet (1960) and Van Horn and Crittenden (1987).

Red Butte sandstone (Nuggett Sandstone) was the first resource utilized from the canyon. Most sandstone was obtained from Quarry Canyon on the south side of the canyon, 4.4 km (2.9 mi) from the mouth of the canyon. Because of the proximity of Quarry Canyon to Salt Lake City, sandstone was quarried there from 1848 to the end of the century by private companies and intermittently by the Army until 1940. This required a road in the bottom of the canyon and housing for workers. In 1889, 66 men and 38 oxen and horses lived at the canyon bottom, contributing considerable downstream pollution to Red Butte Creek. In 1887 the U.S. Congress provided a railroad right-of-way to be built to the rock quarry to increase the amount of sandstone removed. Stream pollution caused by quarrying activity brought many complaints from Fort Douglas and ultimately a court action in 1889, which required the Salt Lake Rock Company to control stream pollution and cease housing men and animals in the canyon.

Red Butte Creek was used for irrigation by a few pioneers east of Salt Lake City in the early 1850s. When Fort Douglas was established in 1862, Army personnel initially depended mostly on water from nearby springs. However, by 1875 Army personnel constructed two reservoirs east of Fort Douglas and diverted water from Red Butte Creek to fill them. In response to the recurrent stream pollution problems caused by quarrying activities, the Territory District Court, in 1890, declared that the waters of Red Butte Creek were the sole property of the U.S. Army and under the jurisdiction of Fort Douglas. Also in 1890, the U.S. Congress passed a law to

TABLE 1. Description of geological formations in Red Butte Canyon.

Cenozoic era, Quaternary system, Holocene series

fa Flood-plain alluvium. Sand, cobbly to silty, dark gray at top; grading downward to medium to light gray, sandy to cobbly gravel; locally bouldery.

fe Engineered fill. Selected earth material that has been emplaced and compacted.

Cenozoic era, Quaternary and Tertiary systems, Holocene and Pleistocene series

fg Alluvial-fan deposits. Bouldery to clayey silt, dark gray to brown; rocks angular to subrounded.

ld Landslide deposits. Composition similar to material upslope.

Mesozoic era, Jurassic system

Jtc Twin Creek Limestone. Brownish gray and pale gray to pale yellowish gray silty limestone, intercalated with greenish gray shale.

Mesozoic era, Jurassic? and Triassic? systems

JTn Nugget Sandstone. Pale pinkish buff, fine- to medium-grained, well-sorted sandstone that weathers orange-brown. Massive outcrops form the ridge called Red Butte.

Mesozoic era, Triassic system

Tau Ankareh Formation, upper member. Reddish brown, reddish purple, grayish red, or bright red shale, siltstone, and sandstone.

Tag Ankareh Formation, Gartra Grit Member. White to pale purple, thick-bedded, crossbedded, pebbly quartzite. Forms a prominent white ledge for long distances.

Tam Ankareh Formation, Mahogany Member. Reddish brown, reddish purple, grayish red, or bright red shale, siltstone, and sandstone.

Tt Thaynes Formation. Medium to light gray, fossiliferous, locally nodular limestone, limy siltstone, and sandstone.

Tw Woodside Shale. Grayish red, grayish purple, or bright red shale and siltstone.

Paleozoic era, Permian system

Ppc Park City Formation and related strata. Fossiliferous sandy limestone, calcareous sandstone, and a medial phosphatic shale tongue.

Paleozoic era, Pennsylvanian system

Pw Weber Quartzite. Pale tan to nearly white, fine- to medium-grained, crossbedded quartzite and medium gray to pale gray limestone.

Prv Round Valley Limestone. Pale gray limestone with pale gray siltstone partings. Contains pale pinkish chert that forms irregular nodules.

Paleozoic era, Mississippian system

Mdo Doughnut Formation. Medium gray, thin-bedded limestone with pods of dark gray to black chert and abundant brachiopods and bryozoa.

Mgb Great Blue Formation. Thick-bedded, locally cliff-forming, pale gray, fine-grained limestone.

Mh Humbug Formation. Alternating, tan-weathering, limy sandstone and limestone or dolomite.

Md Deseret Limestone. Thick ledges of dolomite and limestone with moderately abundant lenses and pods of dark chert.

Paleozoic era

P Paleozoic rocks, undifferentiated.

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protect the water supply of Fort Douglas. This law prevented any sale of land in the canyon or further watershed development. In 1906 the U.S. Army built a dam on Red Butte Creek to supply additional water for Fort Douglas. The present dam was constructed between 1928 and 1930, and the reservoir provided water for Fort Douglas until its closure in 1991.

There are no grazing records available for Red Butte Canyon prior to 1909, by which time the United States had acquired title to most of the land in the canyon. Cottam and Evans (1945) reported evidence of some gully erosion occurring in the canyon prior to 1909 and assumed it was due to overgrazing. Although we lack quantitative data, there are a few isolated incidents indicating the occurrence of grazing, including an 1854 report of a young man drowning in a flash flood in Red Butte Canyon while herding animals. Over forty head of oxen used to haul sandstone from the quarry in the late 1800s remained in the canyon during that time. In 1869 the War Department appointed a herder to control loose cattle grazing on Fort Douglas and in the canyon. In 1890 three squatters had settled into the canyon, and their forty head of cattle were grazing in the Parleys Fork area before being evicted. By 1909 the Army had built a gate at the mouth of the canyon to control access, thus further protecting the watershed. Although this did not prevent occasional animals from wandering into the canyon from adjacent canyons, it did reduce both their numbers and their length of stay. Consequently, most of the canyon has not been grazed by cattle or sheep through most of this century.

Portions of the upper reaches of the canyon were timbered. In 1848, when a road was built along the canyon bottom, it was reported that there was an abundance of timber suitable for fence poles. Later The Church of Jesus Christ of Latter-day Saints built a bowery on Temple Square in downtown Salt Lake City in the 1850s with wood obtained from Table Mound (between Knowltons Fork and Beaver Canyon). In 1863 the Army constructed 34 buildings at Fort Douglas from "timber hauled from the canyons," but there is no indication as to how much timber came from Red Butte Canyon. However, apparently not many timber-size trees were available in the lower canyon as indicated by a pioneer who built a log cabin in the canyon. He stated he had to travel five miles up the canyon to obtain enough logs for the cabin in the early 1860s.

There are no available records of fires that may have occurred in the canyon. In 1988 a fire from Emigration Canyon spread into the upper headwaters of Red Butte Creek before it was contained. The land was subsequently reseeded with native species by the U.S. Forest Service.

Land ownership within the canyon changed several times during the late 1800s and early 1900s. Land occupied by Fort Douglas in 1862 was officially given to the U.S. Army in 1867 when President Johnson withdrew four square miles from public domain for the use of the Army. However, this included only a small portion of the mouth of Red Butte Canyon. The Salt Lake Rock Company, which quarried most of the sandstone in the canyon, owned part of the canyon, and the Union Pacific Railroad Co. acquired four sections in the lower portions of the canyon in the 1860s. Smaller portions of the canyon were claimed by private individuals under the Homestead Act of 1862. Such claims could be acquired easily under this act, which was very liberal and required only a small claim fee. Gradually, between 1884 and 1909, through a combination of acts of Congress, exchanges of property, and outright purchases, Fort Douglas obtained title to most of the canyon by 1896 and almost the entire canyon by 1909. Only three small parcels of a total of less than 90 hectares (~200 acres) are still privately owned today, and these are close to the margins of the canyon. In 1969 the U.S. Department of Defense relinquished ownership of Red Butte Canyon. The U.S. Forest Service is now responsible for these lands. The Forest Service recognized the natural state of the area had been preserved through many years of closure to the public and designated Red Butte Canyon a Research Natural Area in 1970. By definition such areas are tracts of land that have not been strongly impacted by human-related activities such as logging or grazing by domestic livestock. They are permanently protected from devastation by humans so they may serve as reference areas for research and education.

Red Butte Canyon has served as a research site for biologists for over fifty years and will continue to do so in the future. Public education about conservation and the need for the public to better understand the importance of Research Natural Areas are major concerns. Recently the Forest Service briefly opened the canyon to the general public. In 1987 the canyon was opened to the public in late spring for several days; this weekend opening attracted over 5000 visitors and led to a trampling on vegetation along the main road in the canyon. This opening was repeated in 1988 and attracted 1100 people. Currently the State Arboretum at the University of Utah conducts natural history education classes (~10 individuals per group) in the lower portions of the canyon. Limited deer hunting has been permitted by the Forest Service each fall, but the impact of the hunts is unknown. A Red Butte Steering Committee, consisting of representatives from the Forest Service, the University of Utah, and other government agencies concerned with preservation of natural areas, is involved in making decisions pertinent to the jurisdiction and management of the Red Butte Canyon Research Natural Area.

The history of Red Butte Canyon, with the exception of the quarrying activity and some grazing in the past century, is largely a history of preservation. The U.S. Army at Fort Douglas was concerned with the protection of the watershed and gradually acquired sufficient control to protect it. The U.S. Forest Service declared the entire canyon a Research Natural Area and thus insured its protection for the future as a bench mark of riparian and shrub ecosystems in the Intermountain West.

GEOLOGY

The rocks underlying Red Butte Canyon range in age from recent Holocene deposits of our time to Mississippian rocks that are about 360 million years old. Holocene and Pleistocene deposits are unconsolidated, consisting mostly of landslides or alluvium deposited by existing streams. Their aerial distribution is shown in Figure 3, and a description of the deposits is given in Table 1.

The older rocks range in age from Mississippian to Jurassic, a span of about 220 million years. They are all consolidated now, but originally they were formed as deposits in oceans or inland seas or as sand dunes in an arid environment. No rocks representing the approximately 140 million years between the end of Jurassic time and the Holocene are present in Red Butte Canyon. Either they were never deposited or they have been eroded.

The consolidated rocks in most parts of the lower walls of the canyon consist chiefly of shale,

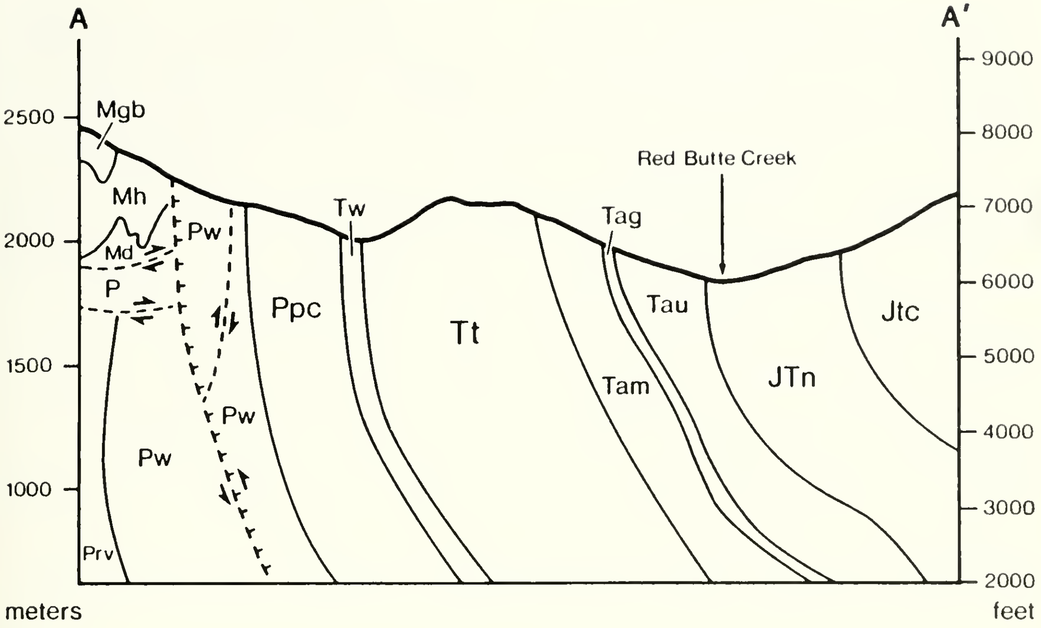

Fig. 4. Geologic cross section of Red Butte Canyon. Explanation as in Figure 3. Adapted from Van Horn and Crittenden (1987).

with some gritty quartzite and sandstone. The upper southeast-facing slopes consist mostly of limestone with some sandstone and limy shale. The upper northwest-facing slopes are made up mostly of sandstone with limestone and limy shale near the southeast divide. Figure 3 shows the distribution of the rocks in the canyon, and they are described in Table 1.

The older consolidated rocks in the canyon generally dip toward the southeast (Fig. 4), and they form the northern flank of a large syncline whose axis trends toward the northeast and whose southern flank is in Mill Creek Canyon, about 6.5 km to the south. The rocks are cut by numerous normal faults that are part of the Wasatch fault zone, a lengthy fault zone that bounds the west face of the Wasatch Range for almost its entire length. Movement along these normal faults has resulted in horizontal displacement of the rock formations, whereas movement along the Black Mountain thrust fault in the northwestern part of the canyon has raised older rocks to a position overlying younger rocks. The faults and their effects on the consolidated rocks are shown in Figures 3 and 4.

SOILS

Soils in Red Butte Canyon are derived from the weathering and erosion of the underlying bedrock. The distribution of the soils in the canyon is shown in Figure 5. The relationship of the soils to the bedrock is apparent by comparing Figure 5 with Figure 3, a geologic map of the canyon. The soils map (Fig. 5) was adapted from Woodward et al. (1974). Soils in Red Butte Canyon have been characterized as dominantly strongly sloping to very steep and well drained. According to Bond (1979), most soils are neutral to slightly basic, vary in color from brick red to dark brown, with textures generally ranging from sandy to loamy clays. Depth of the soil is irregular, with depth to bedrock varying from nearly 2.4 m (94 in) at the canyon floor near the mouth to as little as 60 cm (24 in) or less on the slopes. Soil types include loams, silt loams, and dry loams. There is little profile development, but a pronounced litter layer and appreciable incorporated humus exist in places. Generally the soils are approximately 1 m (39 in) deep, especially those adjacent to streams. However, the steep, rocky upper slopes have shallow and cobbly soils. Table 2 includes a description of each of the soils shown in Figure 5. The descriptions were adapted from Woodward et al. (1974).

HYDROLOGY AND NUTRIENT FLOW

Red Butte Creek is a perennial third-order stream without upstream regulation or diversion

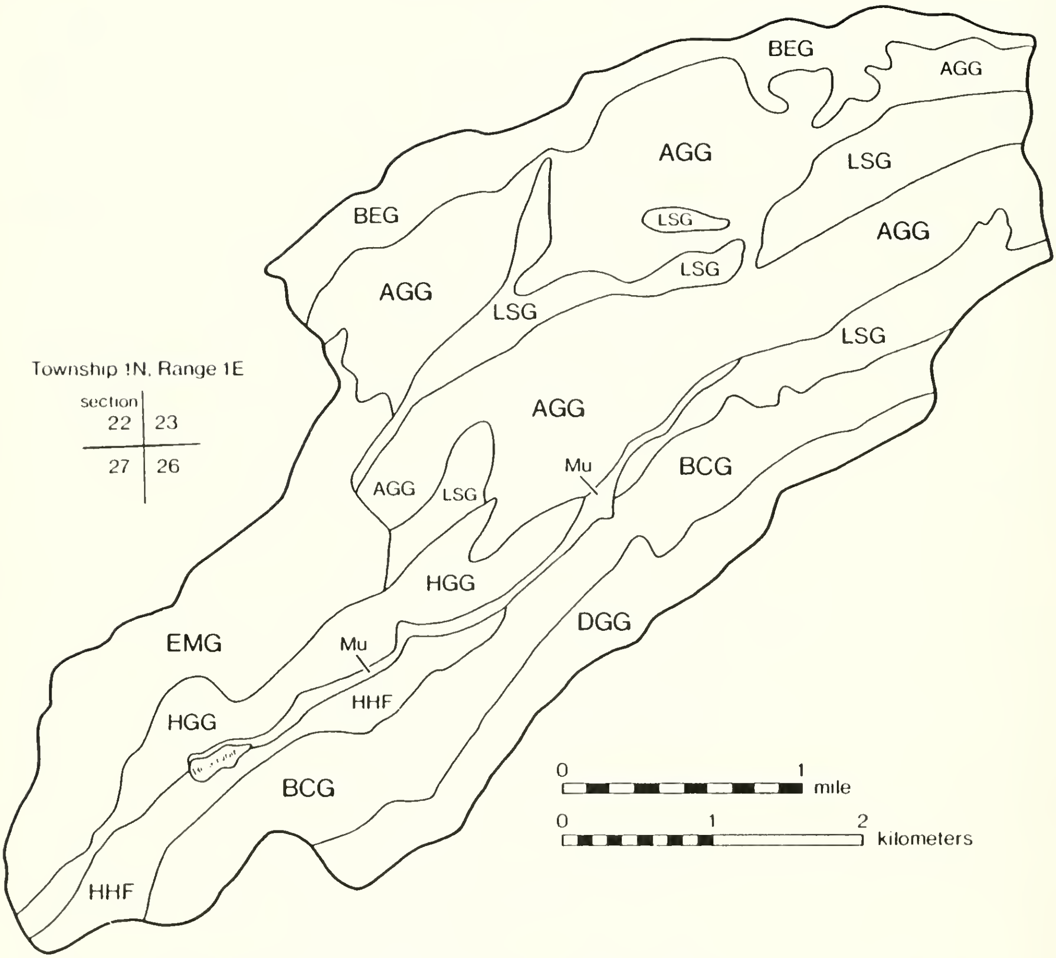

Fig. 5. Soils map of Red Butte Canyon. See Table 2 for a description of abbreviations. Adapted from Woodward et al. (1974).

until flow is collected in the reservoir located near the base of the canyon. The stream has created a narrow-based canyon with sides rising abruptly at an average slope of about 35 degrees to the north and about 40 degrees to the south. Immediately upstream of the reservoir is a U.S. Geological Survey Hydrologic Bench Mark Station. This gaging station has been maintained by the U.S. Geological Survey since October 1963. Prior to that, the Corps of Engineers, U.S. Army, recorded monthly discharge at this location beginning in January 1942.

The average monthly discharge (1964–88) is 0.133 m^3/sec (~4.7 ft^3/sec) as it enters the reservoir at 1646 m (5400 ft) elevation (U.S. Geological Survey records). The stream flow exhibits a straightforward annual pattern, characteristic of this geographic region—high spring flows driven by snowmelt followed by very much reduced flows derived from groundwater throughout the remainder of the year (Fig. 6). Spring melt flow, which is typically an order of magnitude greater than other periods of the year, peaks in May and persists for 6–8 weeks. The average monthly stream flow rate during May is 0.416 m^3/sec (14.7 ft^3/sec). By September, the lowest average monthly flow rate, stream discharge has decreased to 0.058 m^3/sec (2.0 ft^3/sec). Mean stream flow rates do not increase during the summer months, although nearly one-fourth of the annual precipitation falls during this period.

Average monthly stream flow values, however, hide much of the stream dynamics and resultant impact on riparian vegetation. On a daily basis, stream flows can vary tremendously

TABLE 2. Description of units on the soils map of Red Butte Canyon.

AGG Agassiz association, very steep. 40–70 percent slopes; moderately permeable, well drained. Agassiz—35 percent, very cobbly silt loam on ridges and convex areas of upper slopes. Picayune—55 percent, noncalcareous variant, gravelly loam in concave areas and in draws. Other soils—10 percent.

BCG Brad very rocky loamy sand, 40 to 80 percent slopes. Very permeable, extremely well drained. Very rocky, cobbly, loamy sand; dark reddish-brown; shallow.

BEG Bradshaw-Agassiz association, steep. 40–70 percent slopes; moderately permeable, well drained. Bradshaw—55 percent, very cobbly silt-loam in slightly concave areas. Agassiz—35 percent, very cobbly silt-loam in convex areas and ridgetops where soil is shallow. Other soils—10 percent.

DGG Deer Creek–Picayune association, steep. 30–60 percent slopes; moderately permeable, well drained. Deer Creek—55 percent; loam; very dark brown; deep on very steep, north- and northeast-facing mountain slopes. Picayune—35 percent; gravelly clay loam; very dark brown, deep, calcareous on west-facing slopes. Other soils—10 percent.

EMG Emigration very cobbly loam, 40 to 70 percent slopes. Moderately permeable, well drained. Cobbly loam; facing south; dark, grayish brown; shallow; patches of bedrock.

HGG Harkers-Wallsburg association, steep. Moderately permeable, well drained. Harkers—55 percent, loam, 6–40 percent slopes, very dark brown, deep in drainageways and concave areas of slope faces. Wallsburg—35 percent, very cobbly loam, 30–70 percent slopes, on ridges and convex areas of slopes where bedrock is near the surface, very dark grayish brown, shallow. Other soils—10 percent.

HHF Harkers soils, 6 to 40 percent slopes. Moderately permeable, well drained. Loam and cobbly loam, on sloping old alluvial fans and steep mountain slopes.

LSG Lucky Star gravelly loam, 40 to 60 percent slopes. Moderately permeable, well drained. Very dark grayish brown, deep on northerly slpes.

Mu Mixed alluvial land. Poorly drained, highly stratified mixed alluvium on undulating, gently sloping, and nearly level flood plains.

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during snowmelt, depending on air temperatures and snowpack depth (primarily that of upper Red Butte Canyon and Knowltons Fork). The 1982–83 winter was one of unusually high precipitation along the Wasatch Front. Heavy snows in mid-May 1983 were followed by equally unusual warm temperatures at the end of the month. As a consequence, stream flow rates peaked at record values. On 28 May 1983, Red Butte Creek crested at a discharge rate exceeding 2.97 m^3/sec (104.9 ft^3/sec) (stream flow was above the maximum gage height), and overland flow was substantial. This was by far the greatest discharge rate in recent times, having eclipsed the previous maximum single day rate of 1.70 m^3/sec (60.0 ft^3/sec) measured on 18 May 1975 (U.S. Geological Survey Records).

The unusually high stream discharge rate in May 1983 is of particular significance because of its impact on stream geomorphology and adjacent vegetation. The high flows quickly scoured the streambed, taking out beaver dams, eroding stream banks, knocking down riparian trees, and causing massive erosion. Gullies 5–10 m (16–33 ft) deep were cut into permanent streambeds in Knowltons Fork and throughout Red Butte Creek. Sediment flow associated with this record stream discharge was in excess of 269 metric tons (~593,000 lbs) per day in mid-May (compared to typical spring melt concentrations of 1 metric ton [~2200 lbs] per day) (U.S. Geological Survey Records); this resulted in a delta formation at the mouth of Red Butte Reservoir. Prior to the 1982–83 winter, no delta had existed. The delta was soon ~30 m (~100 ft) long. By 1990 the delta had fanned out more than 60 m into the reservoir. The heavy winter rains of 1982–83 saturated soils all along the Wasatch Front, and landslides were common. Red Butte Canyon was no exception. Slope sloughing, which killed the overlying perennial vegetation, was common throughout the canyon. No doubt this compounded the stream sediment load during the spring of 1983 and for several years thereafter. In 1990 signs of the 1982–83 slope sloughing were still clearly obvious in Knowltons Fork as well as in the upper and lower portions of the main canyon. Natural revegetation of both riparian and slope vegetation types has occurred since these floods. In particular, *Acer negundo* (boxelder) and *Salix exigua* (willow) have increased in frequency in the newly deposited alluvium along the streamsides (Donovan and Ehleringer 1991). Recovery of the sloughed slopes, which were for the most part covered by *A. grandidentatum* (bigtooth maple) and *Quercus gambelii* (Gambel oak), has proceeded at a slower rate, with those slopes still dominated by herbaceous species.

As part of the bench mark analysis, the U.S. Geological Survey monitors several major aspects of stream quality in addition to stream discharge, including water temperature, suspended sediment, and chemical quality. Included with chemical quality are specific conductance, pH,

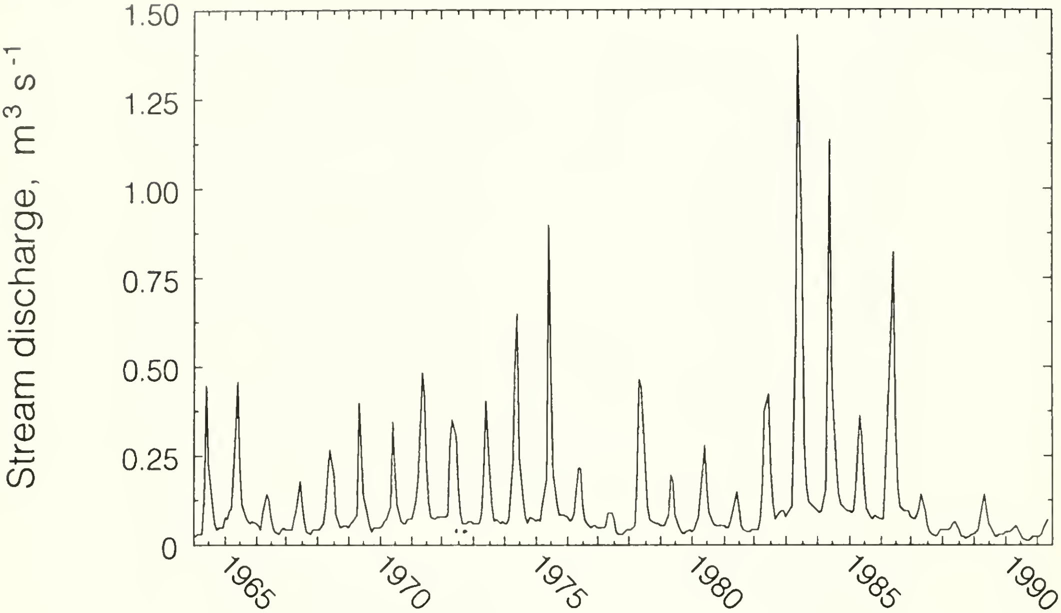

Fig. 6. Mean monthly discharge rates of Red Butte Creek just before it enters Red Butte Reservoir. Large and small tick marks indicate end-of-year and mid-year points, respectively. Data are from U.S. Geological Survey records.

dissolved oxygen concentration, coliform bacteria, and ionic and dissolved elemental concentrations (ammonium, arsenic, beryllium, cadmium, calcium, carbonate, chloride, chromium, cobalt, copper, fluoride, iron, lead, lithium, magnesium, manganese, mercury, molybdenum, nickel, nitrate, nitrite, phosphate, potassium, selenium, silver, sodium, sulfate, strontium, vanadium, and zinc). The stream itself is strongly alkaline (pH 8.0–8.6), and travertine is deposited at several points along the stream channel (Bond 1979).

Summertime stream flow represents groundwater discharge, while the spring flows result primarily from snowmelt at higher elevations. Not all of the groundwater originating from upper-elevation sources enters the stream before it leaves the canyon. Tracing the possible sources of water into stream, and therefore that water which is available to plants, is possible by analyzing the isotopic composition of that water. The deuterium (^2H or D) to hydrogen (^1H) ratios of stream waters have been measured since June 1988 at the USGS Bench Mark station and at the mouth of Parleys Fork by the Stable Isotope Ratio Facility for Environmental Research at the University of Utah (Dawson and Ehleringer 1991). These naturally occurring stable isotopes of hydrogen provide long-term data that are useful in addressing both long-term regional climatic patterns and the specific water sources used by plants for growth (see discussion below). Hydrogen isotope ratios (ratio of D/H of a sample to that of a standard) are measured relative to an ocean water standard; samples lighter than ocean water have less deuterium and are therefore negative in their values. Over the four-year measurement period (1988–91), hydrogen isotope ratios of stream waters have averaged near −122‰, with the only seasonal changes being more negative values occurring during spring snowmelt. Typically the hydrogen isotope ratio of winter storm events (snow) is more negative than that of summer storms. The hydrogen isotope ratios of wells and springs near Pinecrest (immediately east of Red Butte Canyon) are −132‰, slightly more negative than Red Butte Creek (Dawson and Ehleringer 1991), and suggest that a fraction of the groundwater originating from the upper portions of the canyon may persist as underflow and does not enter the creek before leaving the watershed. Hely et al. (1971) indicated that substantial fracturing occurs in the bedrock of Red Butte Canyon, which would have the effect of increasing groundwater loss from the canyon through these layers and not via stream discharge.

Bond (1977, 1979) investigated nutrient-concentration patterns of stream flow in Red Butte Creek. In particular, his studies focused

TABLE 3. Locations of weather stations of Red Butte Canyon. All stations were operated by the U.S. Army between 1942 and 1964, and only precipitation was recorded. The U.S. Geological Survey has maintained a storage gage at Red Butte #2 since 1964. The Biology Department at the University of Utah has maintained daily temperature, humidity, and wind speed records at Red Butte #2, Red Butte #4, and Red Butte #6 since 1982. Red Butte #1, while technically outside the canyon, forms an integrated part of the weather station complex.

Station	Location	Latitude	Longitude	Elevation	Period
Red Butte #1	Fort Douglas	40° 46′	110° 50′	1497 m	1942–1964
	Relocated to Biology Experimental Garden	40° 46′	110° 50′	1515 m	1991–present
Red Butte #2	Head of Red Butte Reservoir	40° 47′	111° 48′	1653 m	1942–1964 1982–present
Red Butte #3	Along Red Butte Creek at Brush Basin	40° 48′	111° 47′	1865 m	1942–1952
Red Butte #4	Along Red Butte Creek 100 m west of Beaver Canyon	40° 48′	111° 46′	1890 m	1942–1971 1982–present
Red Butte #5	Parleys Fork 100 m above inlet to Red Butte Creek	40° 47′	111° 48′	1753 m	1942–1956
Red Butte #6	Upper end Knowltons Fork;	40° 49′	111° 45′	2195 m	1946–1971
	relocated to top of Elk Fork	40° 49′	111° 46′	2195 m	1982–present

on relationships between nutrient transport out of the watershed and stream discharge rates. Solute concentration was not necessarily proportional to stream discharge. Instead, for many ions, such as magnesium, sulfate, and chloride, the relationship was logarithmic. The slopes of these relationships depend on whether stream flow is increasing (i.e., spring snowmelt) or decreasing. Over the course of the year, a loop or directional trajectory was formed by having two different slopes. For most of the major ions, the trajectory was clockwise; that is, ionic concentration was greater in winter when flow rates were low than during summer. Plant growth of the dominant riparian species commences near the end of the snowmelt period, and it is questionable whether riparian species are able to utilize the greater nutrient availability during the snowmelt period. After snowmelt, stream discharge is based primarily on groundwater input. Nitrate, ammonium, and phosphate concentrations in Red Butte Creek during groundwater discharge are low (Bond 1979). In contrast, overall concentrations of calcium, magnesium, sodium, chloride, and sulfate are much greater because of parent bedrock characteristics.

CLIMATE

Climate within Red Butte Canyon is characterized by hot, dry summers and long, cold winters. Most precipitation occurs in winter and spring, with the summer rains less predictable and dependent on the extent to which monsoonal systems penetrate into northern Utah. Mean annual precipitation ranges from about 500 mm (20 in) at the lower elevation to approximately 900 mm (35 in) at the higher elevations (Hely et al. 1971, Bond 1977; Table 3).

Precipitation stations have been monitored in Red Butte Canyon by several groups. The U.S. Army had six rain gages in operation between 1942 and 1964 (Table 3). Bond (1977) collected data at several of these stations between 1972 and 1974. In addition, the U.S. Geological Survey maintained storage gages at Red Butte #2, Red Butte #4, and Red Butte #6 between 1964 and 1974. Since that time, they have maintained a storage gage at Red Butte #2. Within the watershed, daily precipitation as rainfall is collected at each of the weather stations; snowfall is not adequately measured by the sensors in place. However, these data are currently collected at Hogle Zoo in Salt Lake City (same elevation as previous Red Butte #1, but 4 km south).

Variation in annual precipitation within Red Butte Canyon is strongly dependent on elevation (Fig. 7). The slope of this relationship is similar to that observed for other mountainous areas within the Great Basin (Houghton 1969), and precipitation at the Salt Lake City reporting station (Salt Lake City International Airport) falls on this relationship. Thus, while lacking continuous precipitation records for the canyon proper, precipitation records available for Salt Lake City can be used as a preliminary basis for estimating mean annual precipitation at different locations within the canyon.

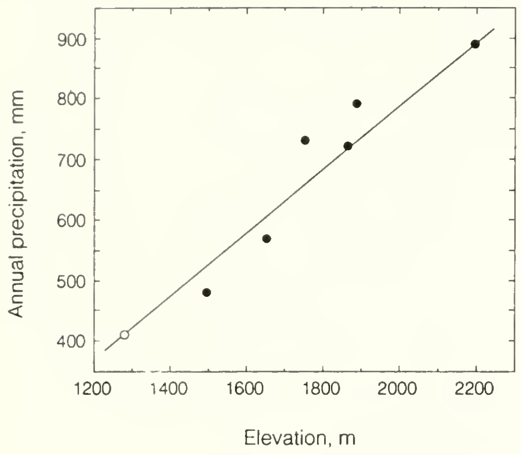

Fig. 7. Relationship between mean annual precipitation and elevation for Red Butte Canyon storage gages Red Butte #1–#6. Shown also is the mean annual precipitation for the primary station of Salt Lake City (Salt Lake City International Airport) as the open symbol.

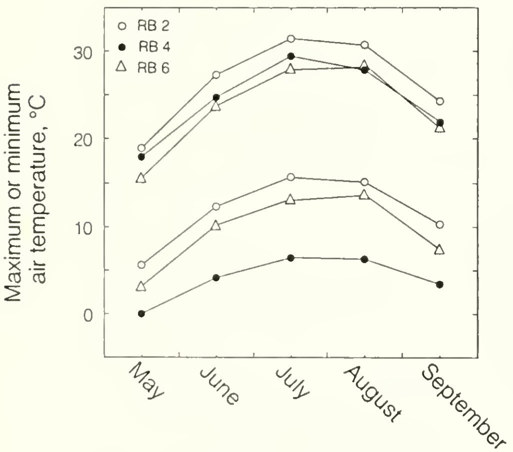

Fig. 9. Mean monthly maximum and minimum air temperature at Red Butte #2 (1653 m elevation), Red Butte #4 (1890 m elevation), and Red Butte #6 (2195 m elevation) during the growing season between 1982 and 1990.

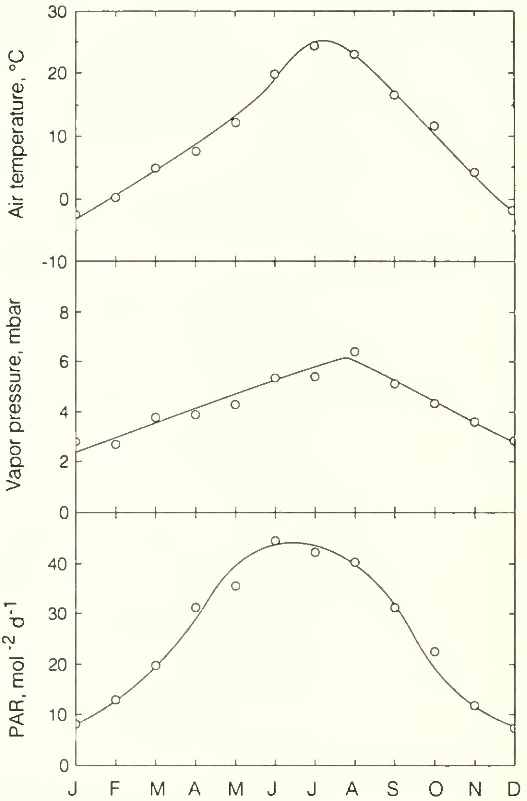

Fig. 8. Mean monthly air temperature, vapor pressure, and photosynthetically active solar radiation (400–700 nm) measured at Red Butte #2 between 1982 and 1990.

Air temperatures have been collected from automated weather stations at Red Butte #2, Red Butte #4, and Red Butte #6 since 1982. Mean monthly air temperatures at Red Butte #2 were below freezing in December and January and above 20 C in June, July, and August (Fig. 8). In contrast, mean monthly temperatures at Red Butte #6 were below freezing only slightly longer, from November through February, and above 20 C in July and August. During the main growing period (May through September), daytime maximum temperatures ranged between 18.7 and 31.8 C (66–89 F) at Red Butte #2, while nighttime minimum temperatures ranged between 5.2 and 16.4 C (41–62 F) (Fig. 9). At the higher-elevation stations, daytime maximum air temperatures were lower. The difference in maximum temperatures was negatively related to elevation (maximum temperature [°C] = 34.3 − 0.00494 · elevation [m], r = .91) at approximately half the dry adiabatic lapse rate. On the other hand, nighttime minimum temperatures were not related to elevation, because of cool-air drainage effects (Fig. 9). Red Butte #4 is located streamside within the canyon, whereas the other two stations are above the channel of cold air that develops at higher elevations and pours down the canyon at night. As seen in Figure 9, this cold-air drainage effect at Red Butte #4 (1890 m [6180 ft] elevation) depressed nighttime minimum air temperatures by 4–8 C (7–14 F) below that observed at Red Butte #6 (2230 m [7292 ft] elevation).

Photosynthetically active solar radiation (PAR, 400–700 nm), atmospheric vapor pressure, and wind speed are also recorded at each of these stations. Between 1982 and 1990, mean daily total PAR values have exceeded 40 mol $m^{-2} d^{-1}$ (Fig. 8), which is typical for mid-latitude sites having only moderate cloud cover and little summer precipitation. This number is quite useful not only in estimating the available photon flux for photosynthesis, but also in providing an estimate of the extent of solar heating of the surface, which ultimately affects air temperatures. Elevation has a limited impact on the PAR values within Red Butte Canyon, since the difference in elevation is relatively small. However, we suspect there may be relatively large differences in PAR between Red Butte Canyon and Salt Lake City because of increased air pollutants within the city that tend to reflect the sunlight before it strikes the earth's surface. Most notably we would see this as haze or smog within the valley that is lacking once in the canyon.

Average monthly atmospheric vapor pressure at site #2 showed little annual variation, ranging only about 3 mbar throughout the year (Fig. 8). Other sites exhibited a similar pattern. This parameter is largely affected by large air mass movements; and since subtropical air masses do not move into this region during the summer, the monthly changes in atmospheric vapor pressure change little during the course of the year. However, because of the large annual change in air temperature and the nonlinear dependence of the evaporative gradient on temperature, relative humidity levels are substantially lower and evaporative gradients are substantially higher during the summer months.

VASCULAR FLORA

From the mouth of Red Butte Canyon at about 1530 m (5020 ft), its walls rise to their highest point—2510 m (8235 ft)—at the head of Knowltons Fork in the northeast corner of the canyon. Within this modest rise of 980 m (3215 ft) occur four distinct plant communities: riparian, grass-forb, oak-maple, and coniferous. Piñon-juniper and ponderosa pine communities, which often occur in this elevational range in Utah (Daubenmire 1943), are not present in Red Butte Canyon. Billings (1951, 1990), in discussions of vegetational zonation in the Great Basin, cites a greater incidence of winter cyclonic storms and slightly more moist summers as factors producing the variation in the vegetative zones of the eastern boundary of the Great Basin. Juniper is present in the central Wasatch Range, but only three Utah juniper (*Juniperus osteosperma*) are known to exist in Red Butte Canyon: a mature tree with a 0.5 m (1.6 ft) diameter trunk, located on the south slope of Parleys Fork and nearly obscured by the more mesophytic vegetation, and two shrublike plants 1–1.3 m (3–4 ft) tall growing on the southwest divide.

With few exceptions, notably the naturalized grasses *Agrostis stolonifera* (redtop bentgrass), *Bromus tectorum* (cheatgrass), and *Poa pratensis* (Kentucky bluegrass), only the most common indigenous plants that occur in the various plant communities are listed below, primarily because the presence of introduced plants is usually dependent on disturbance and tends to fluctuate accordingly. Some of the more frequently occurring introduced plants are listed in a separate section.

RIPARIAN COMMUNITY.—From the point at which Red Butte Creek emerges from the canyon and throughout the floor of the canyon the streamside vegetation (plants residing in soil kept moist to wet by the stream) consists chiefly of western water birch (*Betula occidentalis*) and mountain alder (*Alnus incana*), accompanied at intervals by usually dense stands of red osier dogwood (*Cornus sericea*) and willow (*Salix* spp.). Adjoining the stream along the floor of the canyon below and above the reservoir is an often densely wooded strip consisting chiefly of Gambel oak (*Quercus gambelii*), boxelder (*Acer negundo*), and bigtooth maple (*Acer grandidentatum*), many of these trees ranging from 9 to 18 m (30 to 60 ft) or more tall. Also included in this plant community are widely scattered individuals or small populations of cottonwoods (*Populus fremontii*, *P. angustifolia*, and *P.* × *acuminata*), chokecherry (*Prunus virginiana*), Woods rose (*Rosa woodsii*), bearberry honeysuckle (*Lonicera involucrata*), thimbleberry (*Rubus parviflorus*), serviceberry (*Amelanchier alnifolia*), western black currant (*Ribes hudsonianum*), and golden currant (*Ribes aureum*). Relatively few species of grass and forbs are found here, among them:

Elymus glaucus	blue wildrye
Lomatium dissectum	giant lomatium
Mahonia repens (*Berberis repens*)	Oregon grape
Osmorhiza chilensis	sweet cicely
Poa compressa	Canada bluegrass

P. pratensis	Kentucky bluegrass
Smilacina stellata	wild lily-of-the-valley
S. racemosa	false Solomon-seal
Solidago canadensis	goldenrod

Beaver, once native, were reintroduced into Red Butte Canyon in 1928 (Bates 1963) and were active along Red Butte Creek and some of its tributaries for 54 years thereafter. Numerous marshy areas between elevations of 1645 m (5400 ft) and 2133 m (7000 ft) were created by the impoundment of water due to their dam-building activities. To prevent the beaver populations from becoming undesirably large, the Utah Division of Wildlife Resources in 1971 undertook management of the populations. In December 1981 a recommendation was made, based on an analysis of the water supply to Fort Douglas from Red Butte Canyon, that all beaver be eliminated from the canyon because their feces could contaminate the water with the parasite *Giardia lamblia*. Accordingly, in 1982 the colonel in command of Fort Douglas applied for and received from the Utah Division of Wildlife Resources a permit to remove the beaver from the canyon. Subsequently, all beaver were "harvested."

Bates (1963) studied the impact of beaver on stream flow in Red Butte Canyon. The vegetative cover was affected for approximately 91 m (298 ft) on either side of the portion of the stream in which the beaver were active, and sediment deposited behind the beaver dams in the canyon varied from 0.6 to 2.4 m (2 to 8 ft) in depth. He also noted that the small alluvial plains formed by the sediment made it apparent that during periods of high runoff, and perhaps during normal flow, the dams allowed the retention of quantities of suspended materials. Scheffer (1938), in a report on beaver as upstream engineers, ascertained that two beaver dams retained 4468 m^3 (157,786 ft^3) of silt. It is not known whether an actual count of the number of beaver dams in Red Butte Canyon was ever made; but the environmental change effected by their ultimate displacement during the 1983 flooding of what had to have been enormous quantities of sediment has been significant. The removal of all inactive beaver dams has inevitably led to the elimination of or significant reduction in the density of some 55 species of typically wetland plants from once marshy areas within Red Butte Canyon. For example, in 1990 it was noted that in an area which once supported a nearly pure stand of closely spaced cattails (*Typha latifolia*) covering approximately 0.25 hectare (0.62 acre), only a few scattered clumps remained. According to Forest Service personnel, these losses would not have been as severe had the beaver dams been active during flooding. Species in the following genera are among those undoubtedly affected: *Eleocharis, Scirpus, Juncus, Agrostis, Catabrosa, Deschampsia, Glyceria, Poa, Polypogon, Equisetum, Angelica, Betula, Cicuta, Heracleum, Rudbeckia, Solidago, Barbarea, Cardamine, Nasturtium, Rorippa, Lonicera, Cornus, Trifolium, Mentha, Nepeta, Lemna, Epilobium, Habenaria, Polemonium, Polygonum, Rumex, Aconitum, Ranunculus, Geum, Ribes, Salix, Mimulus, Veronica*, and *Urtica*.

The U.S. Forest Service, Salt Lake Ranger District, requested the Utah Division of Wildlife Resources to reintroduce the beaver during the summer of 1991. At the time of this publication, beaver had not yet been reintroduced. It is hoped that with time the plant diversity typically associated with beaver dams will be reestablished.

GRASS-FORB COMMUNITY.—According to Stoddart (1941), the grasslands of northern Utah form the southernmost extension of the Palouse prairie. Of the two communities into which the Palouse prairie is divided, only that dominated by bluebunch wheatgrass (*Elymus spicatus*, originally known as *Agropyron spicatum*) occurs in Red Butte Canyon. Relatively large open areas inhabited by grasses and forbs, with an occasional big sagebrush (*Artemisia tridentata*), squawbush (*Rhus trilobata*), and bitterbrush (*Purshia tridentata*), are found chiefly below the 1829 m (6000 ft) contour (Kleiner and Harper 1966), although smaller grass-forb associations also occur in forest clearings at higher elevations. Some of the more commonly occurring species within the grass-forb community at lower elevations are:

Achillea millifolium	milfoil yarrow
Allium acuminatum	tapertip onion
Ambrosia psilostachya	western ragweed
Arabis holboellii	Holboell rockcress
Aristida purpurea (*A. longiseta*)	purple threeawn
Artemisia ludoviciana	Louisiana wormwood
Astragalus utahensis	Utah milkvetch
Aster adscendens	everywhere aster
Balsamorhiza macrophylla	cutleaf balsamroot
Balsamorhiza sagittata	arrowleaf balsamroot
Bromus tectorum	cheatgrass
Cirsium undulatum	gray thistle
Collomia linearis	narrowleaf collomia
Comandra umbellata	bastard toadflax

Crepis acuminata	mountain hawksbeard
Cymopterus longipes	long-stalk spring-parsley
Elymus trachycaulus *(Agropyron caninum)*	slender wheatgrass
Epilobium brachycarpum *(E. paniculatum)*	autumn willowherb
Erigeron divergens	spreading daisy
Gutierrezia sarothrae	broom snakeweed
Hedysarum boreale	northern sweetvetch
Heliomeris multiflora *(Viguiera multiflora)*	showy goldeneye
Lomatium triternatum	ternate lomatium
Lupinus argenteus	silvery lupine
Microsteris gracilis	little polecat
Phacelia linearis	threadleaf scorpionweed
Phlox longifolia	longleaf phlox
Poa secunda (P. sandbergii)	Sandberg bluegrass
Stipa comata	needle-and-thread
Wyethia amplexicaulis	mulesears

OAK-MAPLE COMMUNITY.—Gambel oak (*Quercus gambelii*) is the dominant type of vegetation throughout the altitudinal range of the canyon. It forms what appear to be randomly spaced clones throughout much of the area. In accordance with the moisture regimen, the clones may range from thickets 0.3 m (1 ft) or less in height in dry upland sites to stands of stately, well-spaced trees in lowland areas. Both walls of the canyon support often nearly impenetrable oak in association with bigtooth maple (*Acer grandidentatum*), the latter growing chiefly in drainageways. Few species thrive as understory with dense oak cover. The most common are *Galium aparine* (catchweed bedstraw) and *Mahonia repens* (Oregon grape). Others appearing seasonally under oak are *Erythronium grandiflorum* (dogtooth violet), *Claytonia lanceolata* (lanceleaf spring beauty), *Hydrophyllum capitatum* (ballhead waterleaf), and *H. occidentale* (western waterleaf). Among plants commonly fringing oak clones are:

Agoseris glauca	mountain dandelion
Apocynum androsaemifolium	spreading dogbane
Arabis glabra	tower mustard
Bromus carinatus	mountain brome
Comandra umbellata	bastard toadflax
Delphinium nuttallianum	Nelson larkspur
Descurainia pinnata	blue tansy mustard
Eriogonum heracleoides	whorled buckwheat
E. racemosum	redroot buckwheat
Geranium viscosissimum	sticky geranium
Helianthella uniflora	one-headed sunflower
Heliomeris multiflora *(Viguiera multiflora)*	hairy goldeneye
Hydrophyllum spp.	waterleaf
Koeleria macrantha *(K. cristata)*	Junegrass
Leucopoa kingii *(Hesperochloa kingii)*	spike fescue
Lomatium dissectum	giant lomatium
Machaeranthera canescens	hoary aster
Mertensia brevistyla	Wasatch bluebell
Microseris nutans	nodding scorzonella
Phacelia heterophylla	varileaf scorpionweed
Poa fendleriana	muttongrass
P. pratensis	Kentucky bluegrass
Senecio integerrimus	Columbia groundsel

Mountain mahogany (*Cercocarpus ledifolius*) occurs as individuals and as scattered, mostly small populations, often in association with oak, sagebrush, or other mountain shrubs, generally on northwest-facing, sparsely vegetated slopes. It can be seen from the main road through the canyon as small trees against the sky along the exposed, rocky, south rim of the canyon, especially toward its western end. As low shrubs it occurs sporadically, chiefly on exposed dry sites above 1980 m (6500 ft).

Big sagebrush (*Artemisia tridentata*) occurs sporadically in drier sites throughout the canyon's altitudinal range. Low sagebrush (*Artemisia arbuscula*) occurs as relatively pure stands at about 2133 m (7000 ft) along the southeast rim of the canyon.

CONIFEROUS COMMUNITY.—Douglas-fir (*Pseudotsuga menziesii*), white fir (*Abies concolor*), and aspen (*Populus tremuloides*) dominate this community, either in pure or in mixed stands, growing chiefly on north- to northeast- and northwest-facing slopes; the aspen reach as low as 1706 m (5600 ft) and the firs occur mostly above 1828 m (6000 ft). Achlorophyllous *Corallorhiza* spp. (coralroot orchid) are among the few plants able to flourish in the shade of dense stands of mixed conifers. Many small trees, shrubs, forbs, and grasses thrive in less dense stands or in openings between stands of trees in this community. Among them are:

Acer glabrum	Rocky Mountain maple
Amelanchier alnifolia	Saskatoon serviceberry
Aquilegia coerulea	Colorado columbine
Arnica spp.	arnica
Castilleja spp.	Indian paint brush
Ceanothus velutinus	mountain lilac
Elymus glaucus	blue wildrye
Erigeron speciosus	showy fleabane
Galium spp.	bedstraw
Hordeum brachyantherum	meadow barley
Lathyrus pauciflorus	Utah sweetpea
Physocarpus malvaceus	mallow ninebark
Poa nervosa	Wheeler bluegrass
Prunus virginiana	chokecherry
Ribes viscosissimum	sticky currant
Rubus parviflora	thimbleberry
Sambucus spp.	elderberry
Sorbus scopulina	American mountain ash
Symphoricarpos oreophilus	mountain snowberry
Thalictrum fendleri	Fendler meadowrue

PLANTS ENDEMIC TO UTAH.—Only two species occurring in Red Butte Canyon are said to be endemic to Utah: *Angelica wheeleri* Wats. (Mathias and Constance 1944–45) (Wheeler angelica) and *Erigeron arenarioides* (D. C. Eat.) Gray (rock fleabane). *Angelica wheeleri* has, however, been collected close to both the Idaho and the Nevada boundaries with Utah (Albee et al. 1988). *Erigeron arenarioides* is known from Salt Lake, Utah, Tooele, Weber, and Box Elder counties (Albee et al. 1988, Cronquist 1947).

PLANTS INTRODUCED TO UTAH.—In Red Butte Canyon, plants introduced to Utah, either from other portions of the United States or from another country, are largely restricted to roadside and trailside sites and to open grassy or rocky slopes below 1829 m (6000 ft). Some of the more commonly occurring plants in this category are:

Alyssum alyssoides	alyssum
Arabidopsis thaliana	mouse-ear cress
Bromus briziformis (*B. brizaeformis*)	rattlesnake chess
B. japonicus	Japanese or meadow chess
B. tectorum	cheatgrass
Capsella bursa-pastoris	shepherd's purse
Cynoglossum officinale	hound's tongue
Dactylis glomerata	orchard grass
Draba verna	spring draba
Erodium cicutarium	storksbill or alfileria
Grindelia squarrosa	curlycup gumweed
Holosteum umbellatum	jagged chickweed
Isatis tinctoria	dyer's woad
Lactuca serriola	prickly lettuce
Lepidium perfoliatum	peppergrass
Linaria dalmatica	Dalmation toadflax
Lithospermum arvense	corn gromwell
Malva neglecta	cheeses
Melilotus alba	white sweetclover
M. officinalis	yellow sweetclover
Poa bulbosa	bulbous bluegrass
Ranunculus testiculatus	bur buttercup
Sisymbrium altissimum	Jim Hill mustard
Taraxacum officinale	common dandelion
Thlaspi arvense	pennycress
Tragopogon dubius	goatsbeard
Veronica anagallis-aquatica	water speedwell

The incidence of *Isatis tinctoria* and *Linaria dalmatica* increased greatly between 1970 and 1990.

FLORISTIC DIVERSITY.—The following species were reported from Red Butte Canyon by Cottam and Evans (1945) and by Bates (1963). Not only is the presence of these plants unverified by herbarium specimens (see Albee et al. 1988, which is based on specimens in the herbaria of Brigham Young University, Utah State University, and the University of Utah), but at least six of them would not ordinarily occur within the elevational limits of the canyon:

Agrostis semiverticillata	water polypogon
Amsinckia tessellata	rough fiddleneck
Angelica pinnata	small-leaved angelica
**Brickellia grandiflora*	tasselflower
Castilleja angustifolia	Indian paintbrush
Cirsium flodmanii	Flodman thistle
Cryptantha flavoculata	yellow-eye cryptanth
Deschampsia caespitosa	tufted hairgrass
**Erigeron glabellus*	smooth fleabane
**Eriogonum ovalifolium*	cushion buckwheat
Gayophytum ramosissimum	branchy groundsmoke
Geranium bicknellii	Bicknell cranesbill
Glyceria grandis	American mannagrass
Juncus mertensianus	Merten's rush
**Lathyrus brachycalyx*	Rydberg sweetpea
Mentzelia albicaulis	whitestem blazing star
Scirpus maritimus	alkali bulrush
**Stellaria longipes*	long-stalked starwort
Valeriana edulis	edible valerian

The following species were reported by Arnow (1971), but, for the reasons stated below, can no longer be considered part of the flora of the canyon:

Arabis puberula Nutt. (puberulent rockcress)	Collection identified by R. C. Rollins as an anomalous *A. lemmonii* Wats., the correction too late for the 1971 publication.
Calypso bulbosa (L.) Oakes (fairy slipper orchid)	1971 report based on a basal leaf, no subsequent evidence of its presence available.
Carex muricata L. (as *C. angustior* Mack)	A misidentification.

Species names now submerged with those of other species present in the canyon (also included in section on nomenclatural changes):

Arabis divaricarpa A. Nels = *A. holboellii* Hornem.	Holboell rockcress
Bromus commutatus Schrad. = *B. japonicus* Thunb.	Japanese or meadow chess
Glyceria elata (Nash) M. E. Jones = *G. striata* (Lam.) Hitchc.	fowl mannagrass
Juncus tracyi Rydb. = *J. ensifolius* Wikst.	swordleaf rush
Taraxacum laevigatum (Willd.) DC. = *T. officinale* Wiggers	common dandelion

Thus, the 511 species representing 73 families reported from Red Butte Canyon by Arnow (1971) can now be placed at 484 species (390 indigenous and 94 introduced) known to have

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*With the assistance of Kaye Thorne and Leila Shultz, curators of the herbaria at Brigham Young and Utah State universities, respectively, a herbarium check was made to be certain that no Red Butte Canyon specimens exist for those species marked with an asterisk that, according to Albee et al. (1988), are not in Red Butte Canyon or its vicinity.

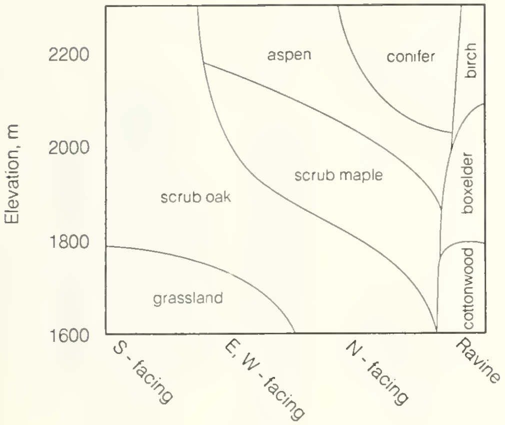

Fig. 10. Distribution, by elevation, of the major plant communities in Red Butte Canyon.

been present in the canyon at one time or another. Only two populations present in 1971 are definitely known to have been eliminated: *Lactuca biennis* (biennial wild lettuce), which was introduced into Utah from the north about 1967 but did not survive; and *Solidago occidentalis* (western goldenrod), a single streamside population at the mouth of the canyon taken out by the 1983–84 flooding.

According to Albee et al. (1988), the 390 indigenous species reported from Red Butte Canyon (Arnow 1971) also occur in at least one other canyon to the south. Arnow et al. (1980) and Albee et al. (1988) indicate that roughly 130 native plants not found in Red Butte Canyon have been collected between an elevation of 1828 and 2438 m (6000 and 8000 ft) in canyons having a greater altitudinal range in southern Salt Lake County. This figure indicates that the floristic diversity in Red Butte Canyon, while greater than that in heavily disturbed Emigration Canyon (Cottam and Evans 1945), is less than that in canyons farther south.

Nomenclatural changes since Arnow (1971) are listed in the Appendix.

PLANT ECOLOGY

VEGETATION DISTRIBUTION.—A number of studies have focused on describing the vegetation distribution within Red Butte Canyon (Kleiner and Harper 1966, Swanson, Kleiner, and Harper 1966, Kleiner 1967). There is a strong xeric to mesic elevation gradient, with lower portions of the canyon dominated by a spring-active grassland community and the upper portions of the canyon typically consisting of summer-active scrub oak, aspen, and coniferous forest communities (Fig. 10). Composition within each of these communities is not constant, but instead species vary in their importance within a community type as orientation and elevation change. These elevation gradients represent a continuum of moisture availability, with high temperatures and low precipitation amounts at lower elevations making conditions more xeric, while slope orientations less southerly in exposure become progressively more mesic within an elevation band. Soil type (Fig. 5) and depth also play a major role in affecting plant distribution by providing variation in the water-holding capacity of the substrate. The distribution of the scrub-oak community to the highest elevations within the canyon is most likely related to soil conditions, since at high elevations scrub oak persists on south-, east-, and west-facing slopes that would normally be expected to be dominated by aspen if it were not for the very shallow, rocky soils that typify these elevations within Red Butte Canyon.

Red Butte Canyon has been largely protected from grazing since its acquisition by the U.S. Army almost a century ago. The consequence of this lack of grazing pressure at lower elevations is a recovery to near pristine levels, and this is clearly reflected in the early community analyses of Evans (1936) and Cottam and Evans (1945). Within the scrub oak and grassland communities of Red Butte Canyon and adjacent Emigration Canyon, a canyon annually exposed to sheep grazing, there are large differences in plant density (Fig. 11). Emigration Canyon was originally described by early pioneers as having a dense vegetation at lower elevations. However, grazing not only reduced that cover but also increased the fraction of the plant cover occupied by ruderal, weedy species (Cottam and Evans 1945). While plant density in Red Butte Canyon may be greater and weedy species composition lower as a result of reduced disturbance and grazing, the canyon is not free of these weedy components and historical effects (as noted in early sections). Dam construction during the 1920s and other U.S. Army activities within the lower portions of Red Butte Canyon have resulted in sufficient disturbance that many ruderal, weedy species, such as *Grindelia squarrosa* (curly gumweed), *Lactuca serriola* (prickly lettuce), and *Polygonum aviculare* (knotweed), are now common.

Samuelson (1950) conducted an analysis similar to that of Cottam and Evans (1945) on the algal components of the streams in Red Butte and Emigration canyons. He observed that as a result of livestock grazing and human settlement, sediment load and turbidity were much greater in Emigration than in Red Butte Creek. The consequence of this stream-quality difference was the dominance by algal genera in Emigration Creek that are turbidity tolerant, such as *Oscillatoria* and *Phormidium*. Conversely, in the clear waters of Red Butte Creek filamentous algae, primarily *Nostoc*, were most common. Overall algal densities were three times greater in Red Butte Creek, owing to the greater light penetration into that stream. At the same time, Whitney (1951) compared the distributions of aquatic insects in the two streams. He found that densities of aquatic insects were greater in Red Butte Creek. Of those insects persisting in Emigration Creek, there was a preponderance of species characterized by gills protected from silt, which would better allow them to tolerate the more turbid conditions in Emigration Creek.

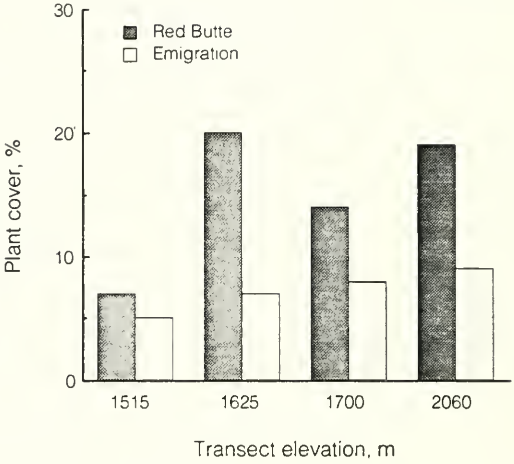

Fig. 11. A comparison of the plant cover in open grassland communities of different elevations in Red Butte and Emigration canyons. Adapted from Cottam and Evans (1945).

PHENOLOGY.—Plant activity is governed by two parameters: temperature and soil moisture availability. Cold winter temperatures limit growth activity between November and March (Caldwell 1985, Comstock and Ehleringer 1992). While a limited number of species, such as the early spring ephemeral *Ranunculus testiculatus* (bur buttercup), may begin activity during warm periods in February, most annuals do not begin growth until the warm periods between snowstorms in early March. At lower elevations, a number of herbaceous perennials such as *Balsamorhiza macrophylla* (cutleaf balsamroot) may begin to leaf out during March, but most woody perennials do not leaf out until mid- to late April. The annuals and most herbaceous species at lower elevations have completed growth and reproduction by mid-June and then remain dormant until the following autumn or spring (Smedley et al. 1991). In contrast, woody species at lower elevations remain active from April through October, although the vast majority of the growth will occur during the spring (Donovan and Ehleringer 1991). At higher elevations, vegetative and reproductive growth are delayed until late May or June by cold temperatures. Plants at the higher elevations will remain active throughout the summer, even though there may be little summer precipitation (Dina 1970, Dina and Klikoff 1973).

ADAPTATION.—In the nonforested portions of the Intermountain West, plant growth is largely restricted to spring and early summer periods by cold temperatures during winter and limited water availability during the summer (Caldwell 1985, Dobrowolski, Caldwell, and Richards 1990, Comstock and Ehleringer 1992). A number of recent reviews have addressed adaptation characteristics of plants growing in these environments (Caldwell 1985, DeLucia and Schlesinger 1990, Smith and Knapp 1990, Smith and Nowak 1990). For the most part, plants within Red Butte Canyon are exposed to a hot, dry environment, with little relief from developing water stress during the summer months. The only clear exception to this pattern is the series of plants within the riparian communities along the canyon bottom. To gain a better understanding of this occurrence, many of the recent ecological researchers within the Red Butte Canyon RNA have focused on mechanisms by which plant species have adapted to limited water availability.

Among the first ecophysiological studies was that by Dina (1970), who examined water stress levels of the dominant tree species in the lower portions of the canyon: *Acer grandidentatum* (bigtooth maple), *Acer negundo* (boxelder), *Artemisia tridentata* (big sagebrush), *Purshia tridentata* (bitterbrush), and *Quercus gambelii* (Gambel oak). Dina (1970) observed that

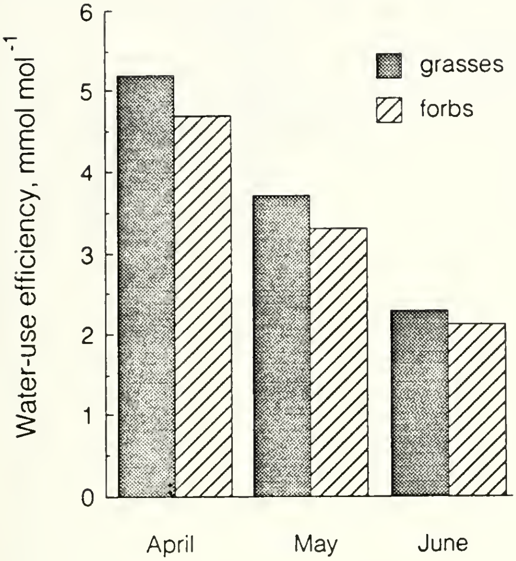

Fig. 12. The mean water-use efficiency values for grasses and forbs within the grassland community of Red Butte Canyon during main period of the growing season. Water-use efficiencies were calculated from carbon isotope discrimination values from Smedley et al. (1991) and the vapor pressure data in Figure 8.

midday leaf water potentials of −30 to −65 bars develop in perennials occupying slope sites during late summer, whereas water potentials of adjacent riparian tree species are maintained between −20 and −30 bars during the same periods. Water potentials in the range of −10 to −15 bars cause many crop species to wilt and close their stomata, reducing transpirational water loss. Tolerance of water stress levels as low as −40 to −60 bars is thought to occur in only the most drought-adapted aridland species. These late-summer water potential values on slope species are sufficiently low to close stomata and reduce photosynthesis to near zero values. In Dina's (1970) study photosynthetic rates of riparian species decreased by 50–80% from nonstress values, but riparian trees were able to maintain positive net photosynthetic rates throughout the summer. More recently, Dawson and Ehleringer (1992) and Donovan and Ehleringer (1991) conducted related studies and again observed that photosynthetic carbon gain of slope species is largely limited to spring and early summer, whereas riparian species are able to maintain photosynthetic rates throughout the year, albeit that photosynthetic rates are lower in summer than in spring.

Two common responses to limited water availability are avoidance and tolerance. Avoidance of water stress is accomplished by completion of growth and reproductive activities before the onset of the summer drought, whereas tolerance is associated with the evolution of features that allow plants to persist through the drought period.

Several interesting studies have been conducted in Red Butte Canyon that shed light onto the nature of a plant's ability to tolerate water stress and persist through time. Treshow and Harper (1974) examined longevity of herbaceous perennials in grass, mountain brush, aspen, and conifer communities throughout the canyon. They observed that life expectancies of dominant herbaceous perennial species, such as *Astragalus utahensis* (Utah milkvetch), *Balsamorhiza macrophylla* (cutleaf balsamroot), *Hedysarum boreale* (northern sweetvetch), and *Wyethia amplexicaulis* (mulesears), are relatively short (3–20 years) when compared to the longer-lived (>65 years) grass species, such as *Agropyron spicatum* (bluebunch wheatgrass) and *Stipa comata* (needle-and-thread). The inability to persist through successive drought years may be one of the reasons that dicotyledonous species have shorter life expectancies than monocotyledonous species. Related to this, Smedley et al. (1991) examined the water-use efficiency of these and other herbaceous grassland species. Water-use efficiency, the ratio of photosynthesis to transpiration, serves as a measure of how much photosynthetic carbon gain occurs per unit water loss from the leaf. Dicot herbaceous perennials had consistently lower water-use efficiencies than their monocot counterparts (Fig. 12). The differences in intrinsic water-use efficiency within this life form may be a major contributing factor to the shorter life expectancy in dicot herbaceous species. Consistent with this pattern, Smedley et al. (1991) observed that water-use efficiency of annual species is significantly lower than that of perennial species in grasslands along the lower portions of the canyon. They also observed that perennials which persist longer into the summer drought period have higher water-use efficiencies than those species that became dormant in late spring. During 1988–90, precipitation was unusually low. The effects of the three-year drought are now seen in Gambel oak and bigtooth maple at their lower distribution limits, especially on shallow soils, where stem dieback has become prevalent.

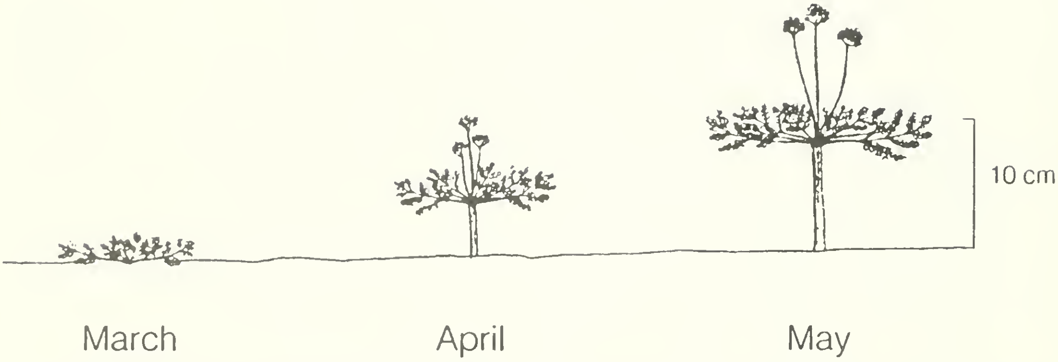

Fig. 13. Height of *Cymopterus longipes* above the ground surface at different months during the spring growing season. After Werk et al. (1986).

Ehleringer (1988) examined leaf-level adaptations of plants along the entire elevational transect within Red Butte Canyon. This study focused on determining patterns of leaf angle and leaf absorptance variation among species within communities exposed to different degrees of drought stress. Increased leaf angle and decreased leaf absorptance reduce the solar energy incident on leaves and are viewed as mechanisms for both reducing leaf energy loads (reducing leaf temperature) and increasing water-use efficiency. Along a transect from grassland through coniferous forest, very few plant species exhibit any significant changes in leaf absorptance. However, leaf angles among species become progressively steeper in drier habitats. This pattern is consistent with the notion that as plants are exposed to progressively drier environments, the general adaptive response of species within the community is to increase leaf angle, thereby reducing incident solar radiation levels.

In the grasslands on the lower portions of Red Butte Canyon is a most unusual plant species, *Cymopterus longipes* (long-stalk springparsley). Sometimes known as the "elevator plant," *C. longipes* is a prostrate herbaceous perennial with an elongating pseudoscape (a scape is a leafless flowering stalk arising from ground level; the pseudoscape is an elongation of the leaf-bearing stem in the region between the roots and existing leaves). Other *Cymopterus* species also have a pseudoscape, but in none of the other species is it as well developed as in *C. longipes*. In spring, solar heating of the ground surface increases soil and leaf temperatures and can result in moderately warm leaf temperatures (30–35 C). These temperatures are substantially higher than the optimum photosynthetic temperature for the elevator plant and result in both a decreased photosynthetic rate and a decreased water-use efficiency (Werk et al. 1986). To increase both the rate of photosynthetic carbon gain and water-use efficiency, the pseudoscape elongates as spring temperatures progressively increase (Fig. 13). The result is that what was once a prostrate canopy is elevated above the warm soil surface and now exposed to cooler air temperatures above the ground surface. Werk et al. (1986) showed that the rate at which the psuedoscape elongates is dependent on the rate of soil-surface heating. Plants from protected or north-facing sites elongate less than those from exposed, southerly sites.

Donovan and Ehleringer (1991) examined relationships between water use and the likelihood of establishment by common shrub and tree species in the lower portions of Red Butte Canyon. They observed that photosynthesis is greater in seedlings than in adults throughout most of the growing season, but that water stress and water-use efficiency are lower in seedlings. Seedling mortality in several of the species is associated with higher water-use efficiencies, suggesting that mortality selection occurs with greater frequency in seedlings that are conservative in their water use before they have established sufficiently deep roots to survive the long summer drought period.

Few studies have addressed ecophysiological aspects of riparian ecosystems in the Intermountain West. This is somewhat surprising since riparian ecosystems are most often among the first to be damaged by human-related activities, from outdoor recreation to water

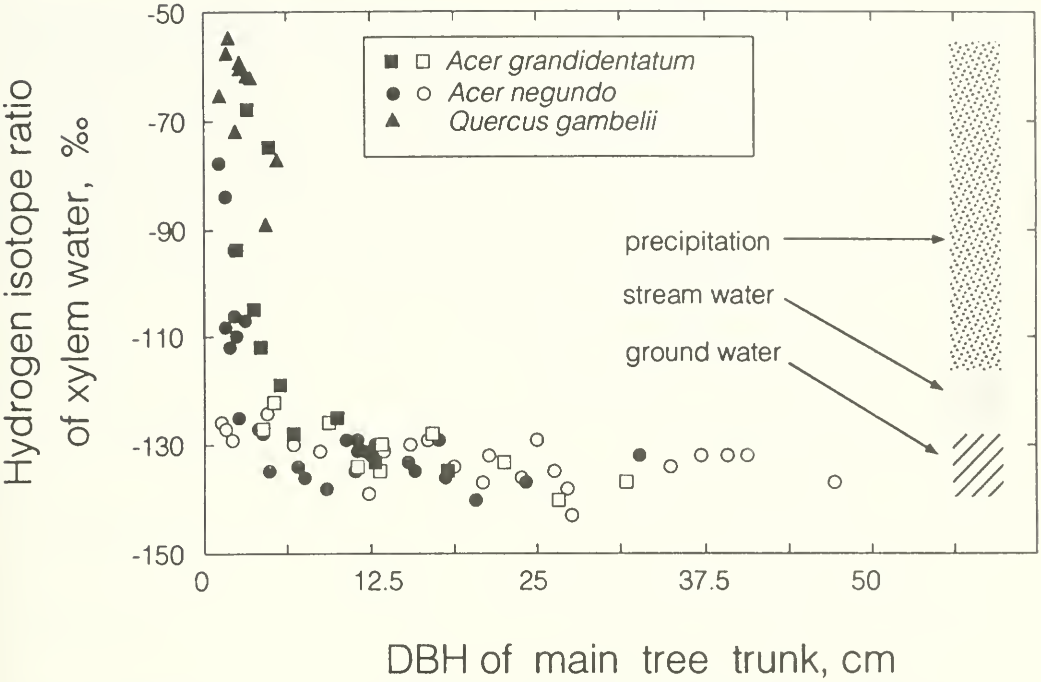

Fig. 14. Hydrogen isotope ratio of stem waters of three common streamside and adjacent nonstreamside tree species in Parleys Fork of Red Butte Canyon as a function of the diameter at breast height of the main trunk. Plotted as gray bars are also the hydrogen isotope ratios of the three possible water sources for these plants: local precipitation, stream water, and groundwater. Open symbols represent streamside plants and closed symbols represent nonstreamside plants. Adapted from Dawson and Ehleringer (1991).

impoundment to grazing. Red Butte Canyon, as one of the few remaining riparian systems in the Intermountain West not severely impacted by human activities, is ideal for studies of the adaptations of riparian plants and for comparative studies of species sensitivities to human-related activities.

In a recent study Dawson and Ehleringer (1992) examined water sources used by riparian plants species. In their study, plants were segregated according to microhabitat and size: streamside versus nonstreamside and juvenile versus adult (based on diameter at breast height). Their results were rather startling and suggest that a new perspective is necessary when evaluating riparian communities, their establishment potentials, and their sensitivity to disturbance. Dawson and Ehleringer (1991) used hydrogen isotope analyses of stem waters to determine the extent to which different categories of riparian trees utilize stream water, recent precipitation, or groundwater. Hydrogen isotopes are not fractionated by roots during water uptake; therefore, the hydrogen isotope ratios of stem water will reflect the water sources currently used by that plant. Rain, groundwaters, and stream waters differ in their hydrogen isotope ratios, providing a signal difference that could be detected by stem-water analyses. Dawson and Ehleringer (1991) observed that among mature tree species none were directly using stream water (Fig. 14). All were using waters from a much greater depth, which had a hydrogen isotope ratio more negative than either stream water or precipitation. Young streamside trees utilized stream water, but only when small. Young trees at nonstreamside locations utilized precipitation, having access to neither stream water nor deeper groundwater. One possible reason that streamside trees may not depend on stream water is that this surface water source may occasionally dry up during extreme drought years and become unavailable to these trees; another is that stream channels occasionally change their course, and dependence on surface moisture would then result in increased drought stress and likely increased mortality rates. The long-term stream discharge rates suggest that stream water may be less dependable than deeper groundwater sources (Fig. 6).

Many plants do not contain both male and female reproductive structures in their flowers, but are present as either male or female plants (dioecy). Freeman et al. (1976, 1980) noted that dioecy is a common feature of plants in the Intermountain West. Furthermore, they observed that the two sexes are usually not randomly distributed across the landscape. Rather there is a spatial segregation of the two sexes such that females tend to predominate in less stressful microsites (wetter, shadier, etc.), whereas males occur with greater frequencies on more stressful sites (drier, sunnier, saltier, etc.). In Red Butte Canyon, Freeman et al. (1976) investigated spatial distributions of *Acer negundo* (boxelder, a riparian tree) and *Thalictrum fendleri* (Fendler meadowrue, a perennial herb). In both species, there was a strong spatial segregation of the two sexes.

Dawson and Ehleringer (1992) have followed up on the initial observations of spatial segregation in *Acer negundo* (boxelder), seeking to determine whether intrinsic physiological differences among the sexes may contribute to plant mortality in different microsites. They observed that female trees have significantly lower water-use efficiencies than male trees on both streamside (where female predominate) and nonstreamside locations (where males predominate). Male trees exhibit a higher water-use efficiency in dry sites than in streamside locations, but female trees exhibit no such response across microhabitats. The lack of a change in water-use efficiency by female trees on dry, nonstreamside locations may contribute to an increased mortality rate, which then ultimately results in a male-biased sex ratio at these sites.

Mammalian Fauna

The mammalian fauna of Red Butte Canyon is remarkably diverse, due in part to the altitudinal gradient and numerous small patches of various plant communities indigenous to the area. A particularly rich small mammal fauna is associated with the patches of riparian habitat along Red Butte Creek and its tributaries. Prior to the run-off of 1983, riparian habitats were much more extensively developed than at present. Numerous marshy meadows existed in association with large, active beaver dams prior to 1982. The loss of active beaver dams in the early 1980s has doubtless greatly reduced the populations of small mammals that are restricted to the mesic-marshy habitats of the canyon.

Nonetheless, based on the altitudinal gradient and vegetational diversity of Red Butte Canyon, a total of 51 species of mammals should hypothetically occur there. Below is a list of the 39 species of mammals known to occur in Red Butte Canyon.

Insectivora—Soricidae	
Sorex palustris	water shrew
Sorex vagrans	wandering shrew
Sorex cinereus	masked shrew
Chiroptera—Vespertilionadae	
Eptesicus fuscus	big brown bat
Lagomorpha—Leporidae	
Lepus townsendi	white-tailed jackrabbit
Sylvilagus nuttallii	Nuttall cottontail
Rodentia—Sciuridae	
Tamiasciurus hudsonicus	red squirrel
Marmota flaviventer	yellow-bellied marmot
Spermophilus armatus	Uinta ground squirrel
Spermophilus variegatus	rock squirrel
Eutamias minimus	least chipmunk
Glaucomys sabrinus	northern flying squirrel
Rodentia—Geomyidae	
Thomomys talpoides	northern pocket gopher
Thomomys bottae	botta pocket gopher
Rodentia—Castoridae	
Castor canadensis	beaver
Rodentia—Muridae	
Reithrodontomys megalotis	western harvest mouse
Peromyscus maniculatus	deer mouse
Peromyscus boylii	brush mouse
Clethrionomys gapperi	red-backed vole
Ondatra zibethicus	muskrat
Phenacomys intermedius	heather vole
Microtus montanus	montane vole
Microtus longicaudus	long-tailed vole
Arvicola richardsoni	water vole
Rodentia—Zapodidae	
Zapus princeps	western jumping mouse
Rodentia—Erethizontidae	
Erethizon dorsatum	porcupine
Carnivora—Canidae	
Canis latrans	coyote
Carnivora—Procyonidae	
Bassariscus astutus	ring-tailed cat
Procyon lotor	racoon
Carnivora—Mustelidae	
Mustela frenata	long-tailed weasel
Mustela erminea	ermine
Mustela vison	mink
Taxidea taxus	badger
Mephitis mephitis	striped skunk
Carnivora—Felidae	
Lynx rufus	bobcat
Felis concolor	mountain lion
Artiodactyla—Cervidae	
Cervus canadensis	elk
Odocoileus hemionus	mule deer
Alces americanus	moose

Some of the larger species have been observed only occasionally, such as the bobcat, mountain lion, and moose. But others such as the mule deer, elk, and coyote are observed with high frequency at some seasons. A rather rich rodent fauna inhabits the canyon, with many of the species preferentially occupying the moist riparian communities of grasses, forbs, and shrubs. Thus, the red-backed vole, heather vole, montane vole, long-tailed vole, water vole, and jumping mouse are virtually restricted to the small mesic meadows along Red Butte Creek and its tributaries. Similarly, the three species of shrews in the canyon are distributed almost exclusively in the riparian habitats.

In some larger meadows, such as along Parleys Fork and at Porcupine Gulch, the microtine rodents are distributed in a strongly zonal pattern. Long-tailed voles are found in the driest parts of the meadows, montane voles in the more mesic areas where grasses, sedges, and forbs comprise a diverse community, and water voles in the immediate streamside area, their burrows often entering the bank at the water's edge. Red-backed voles and heather voles are typically found around the bases of willows in the meadows, as well as around the edges of conifers at higher elevations.

A few species are found only at higher elevations in association with *Pseudotsuga menziesii* (Douglas-fir) and *Populus tremuloides* (aspen). These include the red squirrel, Uinta ground squirrel, yellow-bellied marmot, and least chipmunk. The oak–mountain mahogany zone seems to be the preferred habitat of the rock squirrel and perhaps the ring-tailed cat as well. Several dissertations dealing with the ecology and physiological adaptations of shrews, microtine rodents, and jumping mice have utilized study sites in Red Butte Canyon (Forslund 1972, Cranford 1977).

AVIAN FAUNA

In his study of the birds of Red Butte Canyon, Perry (1973) found that 106 species occurred in the area during his study. Of these, 32 species are permanent residents and 44 are summer residents. The remainder (30) are migrants or winter residents. The permanent resident birds include:

FALCONIFORMES—ACCIPITRIDAE	
Accipiter gentilis	Goshawk
Accipiter striatus	Sharp-shinned Hawk
Accipiter cooperi	Cooper's Hawk
GALLIFORMES—TETRAONIDAE	
Dendragapus obscurus	Blue Grouse
Bonasa umbellus	Ruffed Grouse
GALLIFORMES—PHASIANIDAE	
Lophortyx californicus	California Quail
Phasianus colchicus	Ring-necked Pheasant
Alectoris graeca	Chukar
STRIGIFORMES—STRIGIDAE	
Otus flammeolus	Flammulated Owl
Bubo virginianus	Great Horned Owl
Asio otus	Long-eared Owl
CORACIIFORMES—ALCEDINIDAE	
Megaceryle alcyon	Belted Kingfisher
PICIFORMES—PICIDAE	
Colaptes cafer	Red-shafter Flicker
Sphyrapicus varius	Yellow-bellied Sapsucker
Dendrocopus villosus	Hairy Woodpecker
Dendrocopus pubescens	Downy Woodpecker
PASSERIFORMES—CORVIDAE	
Cyanocitta stelleri	Steller's Jay
Aphelocoma coerulescens	Scrub Jay
Pica pica	Magpie
PASSERIFORMES—PARIDAE	
Parus atricapillus	Black-capped Chickadee
Parus gambeli	Mountain Chickadee
Psaltriparus minimus	Common Bushtit
PASSERIFORMES—SITTIDAE	
Sitta canadensis	Red-breasted Nuthatch
PASSERIFORMES—CERTHIIDAE	
Certhia familiaris	Brown Creeper
PASSERIFORMES—CINCLIDAE	
Cinclus mexicanus	Dipper
PASSERIFORMES—TURDIDAE	
Myadestes townsendi	Townsend's Solitaire
PASSERIFORMES—SYLVIIDAE	
Regulus satrapa	Golden-crowned Kinglet
PASSERIFORMES—STURNIDAE	
Sturnus vulgaris	Starling
PASSERIFORMES—ICTERIDAE	
Sturnella neglecta	Western Meadowlark
PASSERIFORMES—FRINGILLIDAE	
Carpodacus mexicanus	House Finch
Spinus pinus	Pine Siskin
Junco oreganus	Oregon Junco

In addition to the species that are permanent residents in Red Butte Canyon, the following list of summer residents represents species that probably also nest in the canyon:

ANSERIFORMES—ANATIDAE	
Anas platyrhynchos	Mallard Duck
FALCONIFORMES—ACCIPITRIDAE	
Buteo jamaicensis	Red-tailed Hawk
Aquila chrysaetos	Golden Eagle
FALCONIFORMES—FALCONIDAE	
Falco sparverius	Sparrow Hawk
CHARADRIIFORMES—SCOLOPACIDAE	
Actitis macularia	Spotted Sandpiper
COLUMBIFORMES—COLUMBIDAE	
Zenaidura macroura	Mourning Dove
APODIFORMES—TROCHILIDAE	
Archilochus alexandri	Black-chinned Hummingbird
Selasphorus platycercus	Broad-tailed Hummingbird
PASSERIFORMES—TYRANNIDAE	
Empidonax oberholseri	Dusky Flycatcher

Empidonax difficilis	Western Flycatcher
Contopus sordidulus	Western Wood Peewee
Passeriformes—Hirundinidae	
Tachycineta thalassina	Violet-green Swallow
Iridoprocne bicolor	Tree Swallow
Riparia riparia	Bank Swallow
Stelgidopteryx ruficollis	Rough-winged Swallow
Hirundo rustica	Barn Swallow
Petrochelidon pyrrhonota	Cliff Swallow
Passeriformes—Troglodytidae	
Troglodytes aedon	House Wren
Salpinctes obsoletus	Rock Wren
Passeriformes—Turdidae	
Turdus migratorius	Robin
Hylocichla guttata	Hermit Thrush
Hylocichla ustulata	Swainson's Thrush
Sialia currucoides	Mountain Bluebird
Passeriformes—Sylviidae	
Polioptila caerulea	Blue-gray Gnatcatcher
Passeriformes—Vireonidae	
Vireo gilvus	Warbling Vireo
Passeriformes—Parulidae	
Vermivora celata	Orange-crowned Warbler
Vermivora virginiae	Virginia's Warbler
Dendroica petechia	Yellow Warbler
Dendroica auduboni	Audubon's Warbler
Oporornis tolmiei	MacGillivray's Warbler
Wilsonia pusilla	Wilson's Warbler
Passeriformes—Icteridae	
Icterus bullickii	Bullock's Oriole
Molothrus ater	Brown-headed Cowbird
Passeriformes—Thraupidae	
Piranga ludoviciana	Western Tanager
Passeriformes—Fringillidae	
Pheuticus melanocephalus	Black-headed Grosbeak
Passerina amoena	Lazuli Bunting
Carpodacus cassinii	Cassin's Finch
Spinus tristis	American Goldfinch
Chlorura chlorura	Green-tailed Towhee
Pipilo erythrothalmus	Rufous-sided Towhee
Pooecetes gramineus	Vesper Sparrow
Junco caniceps	Gray-headed Junco
Spizella passerina	Chipping Sparrow
Melospiza melodia	Song Sparrow

ROLE OF RESEARCH NATURAL AREAS

Federal land-management agencies have been developing a national system of Research Natural Areas since 1927. More than 400 areas have received this designation nationally. Since inception of the RNA Program, there have been two primary purposes for Research Natural Areas:

1. to preserve a representative array of all significant natural ecosystems and their inherent processes as baseline areas; and
2. to obtain, through scientific education and research, information about natural system components, inherent processes, and comparisons with representative manipulated systems.

Research Natural Areas provide several specific advantages to the nation's scientific community, which are typically not otherwise available. These include potential use of an area that has had minimal human interference and has a reasonable assurance of long-term existence, and the potential association and interaction of scientists from different disciplines leading to discoveries unlikely to occur without such an association. Conducting research at common locations is key to developing these interactions. Research Natural Areas not only assist in the progress of basic science, but also provide federal and state agencies with information upon which to base management decisions. The melding of ecosystem preservation and research on basic ecological processes at Research Natural Areas provides numerous valuable options to society. The Red Butte Canyon RNA serves this purpose well. Although initially affected by human activities during the early settlement of the Salt Lake Valley, the canyon was soon set aside by the federal government and has now had nearly a century to recover (though the loss of beaver represents a significant impact to the ecology of the riparian ecosystem). Other canyons in the Wasatch Range have not received equivalent protection.

As we move into the twenty-first century, there will be increasing pressure to understand the dynamics of ecological systems and man's impact on ecological processes. Maintained as a protected watershed, the Red Butte Canyon RNA provides a unique opportunity for addressing these important issues to human society and to the preservation of our environment. Unprotected, it is an invaluable resource lost forever.

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APPENDIX

Nomenclatural Changes in the Flora, 1971–1990

The following is a list of nomenclatural and orthographic changes made since publication of the Vascular Flora of Red Butte Canyon, Salt Lake County, Utah (Arnow 1971). Family names of flowering plants are changed to accord with those used by Cronquist (1981). All other name changes are contained in Welsh et al. (1987) unless otherwise specified.

AMARANTHACEAE
- *Amaranthus graecizans* of American authors, not L. = *A. blitoides* Wats.

AMARYLLIDACEAE = LILIACEAE
- *Brodiaea douglasii* Wats. = *Triteleia grandiflora* Lindl.

ANACARDIACEAE
- *Rhus radicans* L. = *Toxicodendron rydbergii* (Small) Greene

BERBERIDACEAE
- *Berberis repens* Lindl. = *Mahonia repens* (Lindl.) G. Don

BORAGINACEAE
- *Cryptantha nana* (Eastw.) Pays. = *Cryptantha humilis* (Gray) Pays.
- *Hackelia jessicae* (McGregor) Brand = *H. micrantha* (Eastw.) J. L. Gentry
- *Lappula echinata* Gilib. = *L. squarrosa* (Retz.) Dumort. (Weber 1987)

CACTACEAE
- *Opuntia aurea* Baxter, misapplied to *O. macrorhiza* Engelm.

CARYOPHYLLACEAE
- *Cerastium vulgatum* L. = *C. fontanum* Baumg.
- *Stellaria jamesiana* Torr. = *Pseudostellaria jamesiana* (Torr.) Weber & Hartman (Weber and Hartman 1979)

CELASTRACEAE
- *Pachistima* = *Paxistima*

CHENOPODIACEAE
- *Salsola kali* L. = *Salsola iberica* Sennen & Pau

COMPOSITAE = ASTERACEAE
- *Aster chilensis* Nees = *A. ascendens* Lindl.
- *Haplopappus rydbergii* Blake = *H. watsonii* Gray
- *Lactuca pulchella* (Pursh) DC. = *L. tatarica* (L.) C. A. Mey
- *Matricaria matricarioides* (Less.) Porter = *Chamomilla suaveolens* (Pursh) Rydb.
- *Solidago nemoralis* Ait. = *S. sparsiflora* A. Gray
- *S. occidentalis* (Nutt.) T. & G. = *Euthamia occidentalis* Nutt. (Sieren 1981)
- *Taraxacum laevigatum* (Willd.) DC. = *T. officinale* Wiggers (Weber 1987)

Viguiera multiflora (Nutt.) Blake = *Heliomeris multiflora* Nutt.

Cornaceae

Cornus stolonifera Michx. = *Cornus sericea* L.

Cruciferae = Brassicaceae

Arabis divaricarpa A. Nels. = *A. holboellii* Hornem.

Rorippa islandica (Oed.) Borb. = *R. palustris* (L.) Besser

R. truncata (Jeps.) Stuckey = *R. tenerrima* Greene

Cuscutaceae

Cuscuta campestris Yunck. = *C. pentagona* Engelm.

Cyperaceae

Carex utriculata Boott = *C. rostrata* Stokes

Gramineae = Poaceae (Arnow 1987)

Agropyron caninum (L.) Beauv. = *Elymus trachycaulus* (Link) Shinners

A. dasystachyum (Hook.) Scribn. = *Elymus lanceolatus* (Scribn. & Sm.) Gould

A. intermedium (Host) Beauv. = *Elymus hispidus* (Opiz) Meld.

A. smithii Rydb. = *Elymus smithii* (Rydb.) Gould

A. spicatum (Pursh) Scribn. = *Elymus spicatus* (Pursh) Gould

Agrostis alba L. = *A. stolonifera* L.

A. semiverticillata (Forsk.) C. Christ. = *Polypogon semiverticillatus* (Forsk.) Hylander

Aristida longiseta Steud. = *A. purpurea* Nutt.

Bromus brizaeformis Fisch. & Mey. = *B. briziformis*

B. commutatus Schrad. = *B. japonicus* Thunb.

Glyceria elata (Nash) M. E. Jones = *G. striata* (Lam.) Hitchc.

Hesperochloa kingii (Wats.) Rydb. = *Leucopoa kingii* (Wats.) W. A. Weber

Koeleria cristata Pers. = *K. macrantha* (Ledeb.) Schult.

Oryzopsis hymenoides (R. & S.) Ricker = *Stipa hymenoides* R. & S.

Poa sandbergii Vasey = *P. secunda* Presl (Arnow 1981)

Sitanion jubatum J. G. Smith, misapplied to *Elymus elymoides* (Raf.) Swezey

Stipa occidentalis Thurb. = *S. nelsonii* Scribn.

Juncaceae

Juncus balticus Willd. = *J. arcticus* Willd.

J. tracyi Rydb. = *J. ensifolius* Wikst.

Labiatae = Lamiaceae

Moldavica parviflora (Nutt.) Britt. = *Dracocephalum parviflorum* Nutt.

Leguminosae = Fabaceae

Moraceae = Cannabaceae

Humulus lupulus L. = *H. americanus* Nutt.

Onagraceae

Epilobium paniculatum T. & G. = *E. brachycarpum* Presl

E. watsonii Barbey = *E. ciliatum* Raf.

Oenothera hookeri T. & G. = *O. elata* H.B.K.

Zauchneria garrettii A. Nels. = *Z. latifolia* (Hook.) Greene

Orobanchaceae

Orobanche californica Cham. & Schlecht. = *O. corymbosa* (Rydb.) Ferris

Polemoniaceae

Ipomopsis aggregata (Pursh) V. Grant = *Gilia aggregata* (Pursh) Spreng.

Polypodiaceae, as it occurs in Red Butte Canyon, is now divided into the following families (Tryon and Tryon 1982):

Dennstaedtiaceae, of which the genus *Pteridium* is a member

Dryopteridaceae, which includes the genera *Cystopteris and Woodsia*

Cystopteris fragilis (L.) Bernh. is now known to include two taxa (Lellinger 1985), of which only *C. tenuis* (Michx.) Desv. occurs in Red Butte Canyon.

Ranunculaceae

Ranunculus longirostris Godron = *R. aquatilis* L.

R. testiculatus Crantz = *Ceratocephalus orthoceras* DC. (Weber 1987)

Salicaceae

Salix rigida Muhl. = *S. lutea* Nutt.

Saxifragaceae

Lithophragma bulbifera Rydb. = *L. glabra* Nutt.

Scrophulariaceae

Castilleja leonardii Rydb. = *C. rhexifolia* Rydb.

Tamaricaceae

Tamarix pentandra Pall. = *T. ramosissima* Ledeb.

Umbelliferae = Apiaceae

Cicuta douglasii (DC.) Coult. & Rose = *C. maculata* L.

Lomatium nuttallii (Gray) Macbr. = *L. kingii* (Wats.) Cronq.

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INFLUENCES OF SEX AND WEATHER ON MIGRATION OF MULE DEER IN CALIFORNIA

Thomas E. Kucera[1]

ABSTRACT.—I examined differences by sex and influences of weather on timing and patterns of migration of Rocky Mountain mule deer (*Odocoileus h. hemionus*) in the eastern Sierra Nevada, California, during 1984–87. Deer initiated spring migration from the winter range at about the same time in all years and made extensive use of holding areas at intermediate elevations. Radio-telemetered deer showed strong fidelity to summer ranges over as many as four years. Fall weather produced different patterns of fall migration. Storms during October produced a pulsed migration, in which most animals migrated to the winter range during or soon after the storm; in a year without a storm, fall migration was gradual. Despite the influence of storms on the pattern of fall migration, the median date of fall migration by females did not vary over years; however, among males it was later in a year without fall storms.

Key words: migration, mule deer, Odocoileus hemionus, *sex differences, weather, radio telemetry, California.*

Seasonal migration is common among a wide variety of vertebrates (Baker 1978), including large terrestrial mammals (McCullough 1985, Fryxell and Sinclair 1988). Migration ultimately contributes to individual reproductive success (Baker 1978). Proximally, however, migration is related to the seasonal availability of resources (Sinclair 1983, Garrott et al. 1987). Migration is a common phenomenon among mule deer (*Odocoileus hemionus*) in the mountainous western United States, and various studies have described aspects of mule deer migration (Russell 1932, Leopold et al. 1951, Gruell and Papez 1963, McCullough 1964, Bertram and Rempel 1977, Garrott et al. 1987, Loft et al. 1989). However, questions remain as to the influence of proximate factors, especially weather, on the timing of migration. In addition, because studies of mule deer involving radio-telemetry rarely have included males (e.g., Garrott et al. 1987, Loft et al. 1989), little is known of differences between the sexes in migration patterns.

My objectives were (1) to describe the timing and pattern of seasonal migration of mule deer in the eastern Sierra Nevada, California; (2) to test the hypotheses that there were no differences by sex or year in the timing and pattern of migration and degree of summer-range site fidelity; and (3) to relate observed migration patterns to other aspects of the ecology of these animals.

STUDY AREA

The Sierra Nevada is a massive granite block tilted toward the west, extending for 600 km in a generally northwest-southeast direction (Storer and Usinger 1968). The west side of the mountain range slopes gradually for 75–100 km, from the foothills near sea level to the crest at 3000–4500 m. The eastern Sierra Nevada is more narrow and steep than the west side, with frequent elevational changes of 3000 m in <10 km.

A population of 3000–6000 Rocky Mountain mule deer (*Odocoileus h. hemionus*) winters at the base of the eastern escarpment of the Sierra Nevada in Round Valley, Inyo and Mono counties, California, about 15 km west of the town of Bishop (Fig. 1). An area of about 90 km^2 of Round Valley is used by mule deer as winter range, at elevations from about 1450 to 2100 m. Pine Creek forms the dividing line between what is termed the Sherwin Grade (SG) deer herd to the north and the Buttermilk (BM) herd to the south. These deer are hunted under bucks-only regulations, and posthunt adult sex ratios of 7–12 males:100 females occurred during this study (California Department of Fish and Game, Bishop, California).

As winter storms from the Pacific Ocean rise up the western slope of the Sierra Nevada, they deposit moisture, leaving a much more arid rain shadow on the east side. Precipitation in the

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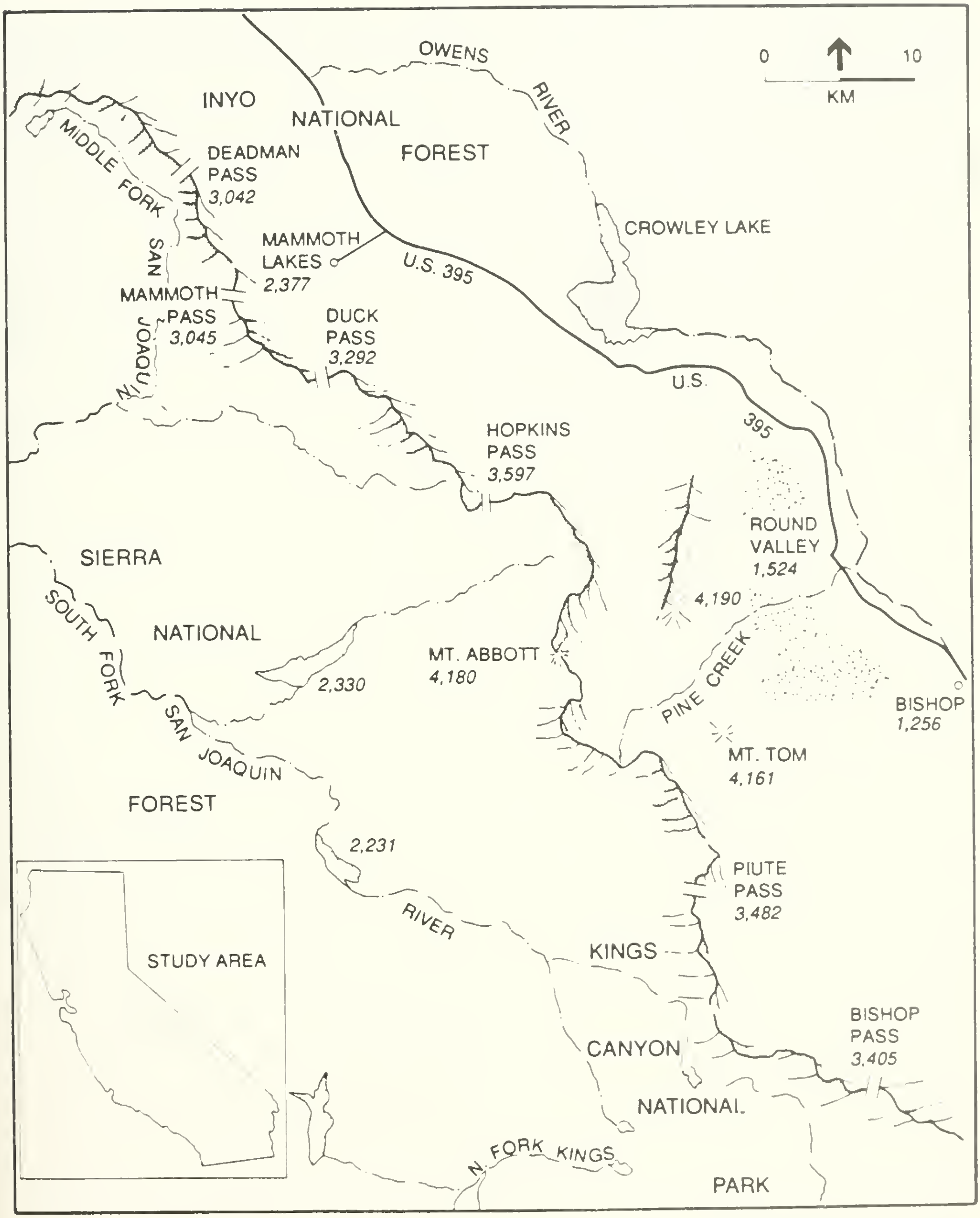
OWENS RIVER
0 10
KM
INYO NATIONAL FOREST
MIDDLE FORK SAN JOAQUIN
DEADMAN PASS 3,042
MAMMOTH LAKES 2,377
MAMMOTH PASS 3,045
DUCK PASS 3,292
U.S. 395
CROWLEY LAKE
U.S. 395
HOPKINS PASS 3,597
ROUND VALLEY 1,524
SIERRA NATIONAL FOREST
SOUTH FORK SAN JOAQUIN
4,190
2,330
MT. ABBOTT 4,180
PINE CREEK
BISHOP 1,256
MT. TOM 4,161
2,231
PIUTE PASS 3,482
RIVER
KINGS CANYON NATIONAL PARK
BISHOP PASS 3,405
N. FORK KINGS
STUDY AREA

Fig. 1. Map of the study area showing the deer winter range as the shaded area in Round Valley; the crest of the Sierra Nevada is from northwest to southeast, with elevations (m) of selected peaks and major passes.

area ranges from an annual mean of 14.5 cm at the Bishop airport at 1240 m to 40.6 cm at 2860 m in Pine Creek Canyon (Vaughn 1983, National Oceanic and Atmospheric Administration 1987). Precipitation is strongly seasonal, with about 75% of the annual total occurring between November and March. Summers are hot, with daytime temperatures in July often >37 C. January is the coldest month, with an average temperature of 4 C and frequent nighttime lows of <-15 C. Potential evapotranspiration is 66.8 cm, or more than four times the mean precipitation.

Vegetation on the winter range is typical of the Great Basin Desert and conforms to the sagebrush belt of Storer and Usinger (1968). Shrubs are dominant, and blackbrush (*Coleogyne ramosissima*), rabbitbrush (*Chrysothamnus* spp.), big sagebrush (*Artemisia tridentata*), and antelope bitterbrush (*Purshia tridentata*) are most common. Deer summer ranges are on both sides of the Sierra crest, at elevations from about 2200 to >3600 m (Kucera 1988), and include the sagebrush, jeffrey pine (*Pinus jeffreyi*), lodgepole pine (*P. murrayana*)–red fir (*Abies magnifica*), subalpine, and alpine belts (Storer and Usinger 1968).

Livestock use of deer winter range was light, consisting of 129 animal-unit-months of use by cattle, restricted to part of the SG range from 1 April to 15 October (U.S. Department of the Interior 1990). Use of deer summer areas by livestock (including horses, cattle, and sheep) varied from very heavy in more accessible locations on the east side of the mountain range to none at higher elevations and more remote areas.

METHODS

Fieldwork was conducted from January 1984 through May 1987. Deer were captured on the winter range January through March 1984 and January and February 1985 with a variety of methods including Clover traps (Clover 1956) baited with alfalfa, drive nets using a helicopter, and remotely triggered drop-nets; net guns fired from a helicopter and tranquilizer darts also were used to capture selected males. Deer captured in 1984 in Clover traps were chemically immobilized with Rompon (xylazine hydrochloride), the effects of which were reversed with yohimbine after handling (Jessup et al. 1985). Deer were captured also during May 1984 and 1985 with tranquilizer darts on a spring migration "holding area" (Bertram and Rempel 1977) about 50 km north of the winter range. This is an area where deer congregate for 2–6 weeks before continuing to areas occupied during the summer.

I fitted 8 males and 9 females from the BM winter range, 7 males and 10 females from the SG winter range, and 10 females captured on the spring holding area with radio collars (Telonics Inc., Mesa, Arizona). All deer were ≤2.5 years of age. I attempted to distribute capture efforts throughout accessible areas to minimize biases in the marked sample. I selected females for telemetry to include all age classes of adults; however, I selected males to receive radio collars on the basis of large size and relatively old age. I excluded smaller, younger males because of concerns arising from body growth; males do not approach maximal neck circumference until about 4 years of age (Anderson 1981), and this, combined with seasonal neck swelling during rut, could result in injury caused by radio-telemetry collars. Older males have achieved nearly maximum body growth; I allowed for seasonal neck swelling by attaching the nonexpandable collars with a circumference 20–25% larger than the animal's neck circumference after rut, measured midway between head and shoulders. I noticed no serious problems resulting from the use of radio collars on male deer in this study, although after a year or two, some fur appeared to be rubbed off the backs of the necks; a similar situation occurred with telemetered females. Collars on the males moved toward the head when the necks swelled during rut and hung loosely at other times.

While animals were on the winter range, I determined at least once per week, and usually more often, whether each radio-marked animal was on the BM or SG winter range by observing the direction of transmitter signals received from standard locations. These data were supplemented by additional radio locations and visual locations as observers moved through the winter ranges. During spring and fall migrations, and during summer, locations of telemetered deer were determined from a fixed-wing aircraft, from a vehicle, and from the ground. During the spring, locations were determined several times per week until the animals crossed the crest of the Sierra. Due to the remoteness of most summer ranges in roadless wilderness areas, frequency of locations of animals, determined from the air and the ground, on the west side of the Sierra Nevada was approximately twice per month. Of 42 deer that reached summer ranges, I located 38 from the ground.

Twenty-two deer were followed for more than one summer. Of these, 10 (45%; 1 male, 9 females) were located in two consecutive summers, 9 (41%; 3 males, 6 females) in three consecutive summers, and 3 (14%; 1 male, 2 females) in four consecutive summers. For these animals I expressed fidelity to summer range as the greatest linear map distance between mean locations in consecutive summers (1 July–7 September). During the fall, locations of animals were monitored from the east side of the Sierra crest at least several times per week, and frequently daily. I could thus determine, within several days and often within one day, when telemetered deer from the west side of the crest crossed to the east side.

I divided annual migration into three periods: (1) leaving winter range, defined as ascending to an elevation >2100 m; (2) crossing the Sierra Nevada crest in spring; and (3) crossing the crest in fall. The last two apply only to those animals ($n = 34$) that summered west of the crest. Because of logistic difficulties in locating animals on the west side of the crest, I did not attempt to determine precisely when animals crossing the crest reached their summer ranges. The steep eastern slope of the Sierra Nevada provided the opportunity to determine the presence or absence of a radio-marked animal on the east side with little error. In situations in which I could not determine an exact date of crossing, I estimated the date as the midpoint of the interval in which I did and did not receive a signal.

For analysis I determined frequencies of movement by week during an 8-week period of leaving the winter range beginning 1 April, a 7-week period of crossing the crest in spring beginning 15 May, and an 11-week period of crossing the crest in fall beginning 11 September. I used the Kolmogorov-Smirnov test with chi-square approximation (Siegel 1956) to test for sex differences in the timing of these components of migration. Steep mountains on the west side of Round Valley constrained movement off the winter range to northerly or southerly routes; I tested for sex differences in the direction (north or south) of migration from the winter range with the binomial test (Zar 1984:591). I expressed temporal patterns of fall migration as the percentage of radio-marked deer in an annual sample crossing the crest during any week. I tested for differences among years in the largest weekly percentage crossing the crest in any year with the Z-test (Zar 1984:396).

From April through June of 1985, 1986, and 1987, commencing as soon as snow conditions permitted, deer were counted from a vehicle along a standardized route of 11 km that passed through a major spring holding area located 1–8 km south of the town of Mammoth Lakes, approximately 50 km north of the winter range. These weekly surveys began 30 minutes before sunrise, and direction of travel was alternated on consecutive surveys.

Daily precipitation in the fall was measured at the U.S. Forest Service (USFS) weather station at the Mammoth Lakes Ranger Station, Inyo National Forest, Mammoth Lakes, California, at an elevation of about 2400 m. Winter snowfall totals were from the USFS weather station on Mammoth Mountain, at about 2940 m.

RESULTS

Spring Migration

From 1984 to 1986 the first radio-marked deer left the winter range during the first or second week of April in any year; in the same years the last radio-marked deer left during the second, third, and fourth weeks of May. For females the median departure date from the winter range was during the third, second, and third weeks of April 1984–86, respectively; for males, the median was during the second week of May and second and third weeks of April, respectively. The frequency differences by sex in weekly migration approached statistical significance ($X^2 = 5.94$, df = 2, $.05 < P < .10$).

Of the 17 telemetered deer from the BM range, 10 (3 of 8 males, 7 of 9 females) migrated north, through the SG range, to reach their summer range; 5 males and 2 females moved south. Of the 17 deer telemetered on the SG range, 15 (5 of 7 males, 10 of 10 females) migrated to the north; 2 males went south. Overall, more ($P = .0003$) females migrated north ($n = 17$) than south ($n = 2$). Analysis by herd showed a significant difference ($P = .0001$) in migration direction among SG females ($n = 10$); the difference among BM females ($n = 9$) approached statistical significance ($P = .07$). There were no significant differences among males in migration direction, either with all males combined ($n = 15$, $P = .196$), or by herd (BM: $n = 8$, $P = .22$; SG: $n = 7$, $P = .16$). Of the 10 females captured on the spring range, 4 wintered on the BM range, 5 wintered on the SG range, and 1 died before the fall migration.

Holding Areas

After leaving the winter range, telemetered deer moved to higher-elevation holding areas at

2200–2400 m on the east side of the Sierra Nevada. Hundreds of deer already were present on the first road surveys of the spring, and patterns of occurrence were similar in all years (Fig. 2). Largest numbers were counted in late April and early May; numbers then decreased through mid-June as deer moved to summer ranges. During early spring a portion of the wintering animals also foraged in irrigated meadows immediately adjacent to the winter range in Round Valley.

Diminution of deer counted on the holding area was reflected by an increase in deer crossing the crest to summer ranges. Of the radio-marked deer that summered west of the crest, the first crossed the crest during the third or fourth week of May in any year, and the last crossed during the third or fourth week of June. There were no sex differences in timing of spring crossing ($X^2 = 3.50$, df = 2, $P > .10$). The median for both sexes in all years was the first week of June.

The temporal uniformity over years in leaving the spring holding area for summer ranges occurred despite greatly different snow conditions. In the winters of 1983–84, 1984–85, and 1985–86, the USFS recorded total snowfalls of 671, 767, and 1021 cm, respectively, on Mammoth Mountain, geographically close and at an elevation similar to the passes that migrating deer crossed to reach summer ranges on the western slope. Despite these differences in snowfall and consequent snowpack at higher elevations, no differences in the timing of spring migration were evident. The snowfall of winter 1986–87 was only 246 cm, or less than one-quarter of that of the previous year. Although the sample size is small, the median week that three radio-marked males and two radio-marked females crossed the crest in the spring of 1987 was the same as the previous year, the first week of June. Thus, the amount of snow on the ground did not appear to influence the timing of migration over the Sierra crest in the spring.

Summer Range

Of the 32 deer captured on the winter range that reached summer ranges, 28 (87.5%) crossed the Sierra crest and summered on the west side. Summer range locations of these deer, plus those of deer captured on the spring range, extended from the headwaters of the Middle Fork of the San Joaquin River south throughout the upper San Joaquin River drainage above about 2134 m into the North and Middle forks of the Kings River (Kucera 1988). Two males and 4 females summered on the east side of the Sierra, from Mammoth Pass on the north to the North Fork of Bishop Creek on the south. Thus, an area nearly 100 × 25 km served as summer range for deer from the BM and SG herds.

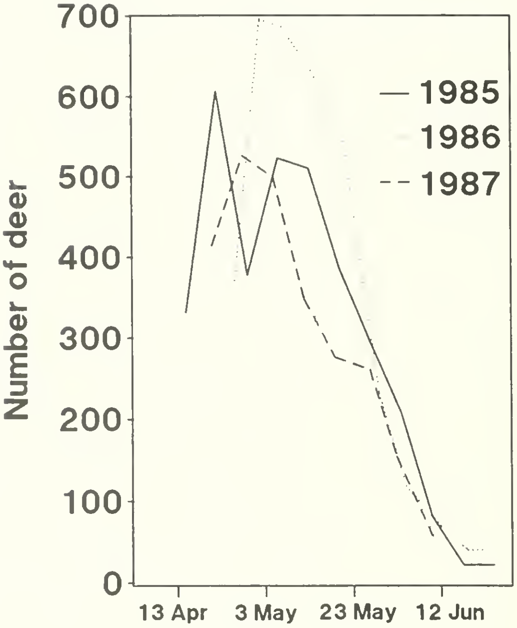

Fig. 2. Number of mule deer counted from a vehicle on standardized weekly surveys at dawn through a spring holding area near the town of Mammoth Lakes, Mono County, California, 1985–87. Surveys began in the spring when snow conditions made the roads passable.

Summer Range Fidelity

Distances between summer ranges of 22 deer located in consecutive years averaged 0.7 km (range = 0.2–4 km) for both males ($n = 5$) and females ($n = 17$). Only 1 deer, a female, was >1 km from a previous location in successive summers; she spent her second summer about 2.5 km from her first, and her third and fourth about 1.5 km farther away.

Fall Migration

In 1984, 1985, and 1986 the first radio-marked deer crossed to the east side during the first week of October and second and fourth weeks of September, respectively; all were females. The last crossed during the fourth week of October and second and fourth weeks

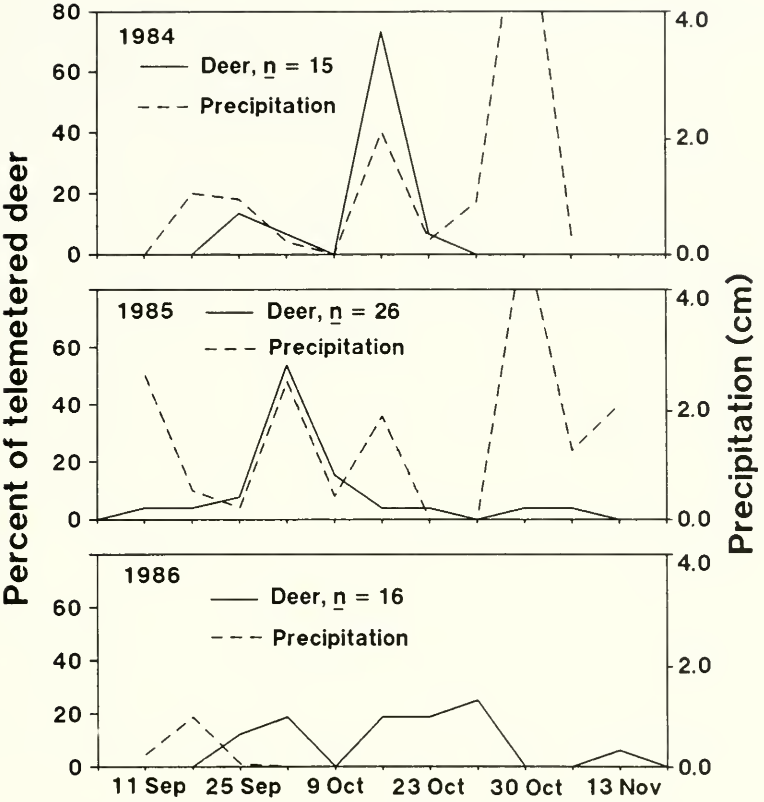

Fig. 3. Percentage of telemetered mule deer per week crossing the crest of the Sierra Nevada, Inyo and Mono counties, California, and weekly precipitation measured at the town of Mammoth Lakes, Mono County, in the fall of 1984–86.

of November; all were males. In 1984 and 1985 the median week of crossing the crest was the same for both sexes, the third and second weeks in October, respectively. In 1986 the median for females was the third week in October, but was two weeks later for males ($X^2 = 18.72$, df = 2, $P < .001$).

Length of time during which fall migration occurred also varied among years. In 1984, 11 of 15 (73%) and, in 1985, 14 of 26 (54%) telemetered deer, including both sexes, crossed the crest in a one-week period. These proportions were not different ($Z = 1.2$, $P > .11$). However, in 1986 no more than 4 of 16 (25%) radiomarked deer crossed the Sierra crest in any week. This proportion was smaller than those of the previous two years ($Z = 2.45$, $P < .007$), indicating that in 1986 there was no mass movement of deer in a short time period.

Differences among years both in timing and in pattern of fall migration were related to the presence or absence of major fall storms (Fig. 3). In 1984, 1.8 cm of precipitation in the form of about 20 cm of snow was recorded on 17 October at Mammoth Lakes; no doubt snow at the passes (400–1500 m higher) used by migrating deer was much deeper. This storm was accompanied by a rapid movement of radiomarked deer over the crest and to the winter range within a few days. Earlier storms, which resulted in virtually no snow at the recording station, did not trigger movement. In 1985, shortly after a storm on 7 October, there was another rapid movement of deer over the crest. The remaining deer appeared gradually on the east side of the crest through 13 November, when the last radioed animal, a male, migrated over the crest following a major winter storm. In both 1984 and 1985 I saw dozens to hundreds of deer migrating simultaneously with the telemetered animals, and many tracks and deep trails in the snow were evident. In 1986 there were no major fall storms. Migration was gradual and unpunctuated by any rapid, mass movements (Fig. 3). In all cases deer returned to the winter range (BM or SG) occupied in previous years.

DISCUSSION

In this study the timing of mule deer migration from the winter range did not differ among years. This occurred despite large differences in animal condition and vegetation growth measured on the winter range (Kucera 1988). One explanation may be that these deer had well-defined spring holding areas where they could predictably obtain nutritious forage, available even in years of heavy snowfall such as 1986, when hundreds of deer were on the holding area when counts began (Fig. 2).

Adult males may leave the winter range somewhat later than females, as reported from western Colorado (Wright and Swift 1942). Given the demands of pregnancy, females might be under greater nutritional stress than males, and if better forage conditions exist on spring ranges, females may tend to leave the winter range sooner to take advantage of them. Garrott et al. (1987) reported that spring migration of female mule deer in northwest Colorado varied between years by as much as one month, and they attributed these differences to the severity of winters and consequent energetic demands on deer. Bertram and Rempel (1977) reported that California mule deer (*O. h. californicus*) on the western slope of the Sierra Nevada varied the timing of their spring migration by two weeks, and attributed this to differences in plant phenology both on the winter range and along the migration route. Loft et al. (1989) also reported a similar relationship between initiation of spring migration and amount of snow and stage of plant growth in the western Sierra Nevada.

In my study most telemetered females migrated from the winter range to the north; males showed no significant selection for direction. I contend that this sex difference is a product of local geomorphology and land management patterns. Animals moving north had access to an extensive area of the west slope of the Sierra Nevada on national forest lands at elevations of 2200–2800 m. Animals moving south had access to summer range in King's Canyon National Park at higher and steeper, and thus more barren and less vegetated, elevations (Kucera 1988). The presence of more and better summer range to the north explains why most deer of both sexes would migrate to the north. However, those animals migrating to the north were in areas open to hunting both on their summer ranges and along the migration routes. That telemetered males showed no apparent selection for migration direction, whereas most females migrated to the north, probably resulted from the higher hunting mortality of males summering to the north, and the absence of hunting in the national park. Although as many males as females would be expected to migrate to the north, the higher mortality of adult males moving north could explain the apparent pattern of no directional preference. Because older males are disproportionately reproductively successful (Kucera 1978, Geist 1981, Clutton-Brock et al. 1982), the national park may act as a refuge for a large proportion of the most reproductively successful males.

Deer in this study made extensive use of holding areas in the spring (Fig. 2), which may be beneficial because of higher elevation, greater precipitation, and absence of winter feeding. Vegetation in these holding areas was largely sagebrush scrub (Munz and Keck 1959), a common vegetation type in the eastern Sierra Nevada. These areas are among the last large areas with vegetation suitable for deer present in the spring before the deer cross the Sierra crest. Large aggregations of deer on the holding areas may result from animals simply collecting in these areas for several weeks before ascending over the crest. Bertram and Rempel (1977) and Loft et al. (1989) described a similar pattern of use of spring ranges in the western Sierra Nevada and emphasized the importance of these holding areas in providing herbaceous forage. Further, Bertram and Rempel (1977) reported that spring holding areas typically occurred at the base of an abrupt elevation change, which was true in my study.

Timing of movement off the holding area and over the crest in spring did not differ among years or between sexes, suggesting that animal condition or vegetation did not greatly affect this stage of migration. The passes had snow in all years of study when deer crossed, but snow depths differed greatly. However, by spring snow was consolidated, enabling deer to walk over the surface.

In 1951 Jones (1954) found that BM deer began moving off the winter range about 1 April, and began crossing a nearby pass about 15 May.

This agrees well with the present observations made more than three decades later. In the western Sierra Nevada, Russell (1932), Leopold et al. (1951), Bertram and Rempel (1977), and Loft et al. (1989) described spring migration as an "upward drift" of deer, controlled by the receding snowline and spring plant growth. My study showed a different pattern in the eastern Sierra Nevada. The upward movement of deer was blocked by the abrupt elevation change of the mountains. On the more gently sloping west side, deer can follow spring gradually up slope. On the abrupt east side, the need to cross high-elevation passes prevents such a pattern.

The strong fidelity to specific summer home ranges shown by individual deer in this study is characteristic of mule deer (Ashcraft 1961, Gruell and Papez 1963, Robinette 1966, Bertram and Rempel 1977, Garrott et al. 1987, Loft et al. 1989). With few exceptions, both males and females returned to the same summer home ranges, and winter ranges, for as many as four consecutive years.

The temporal pattern, pulsed or gradual, of the fall migration in the eastern Sierra Nevada is largely determined by weather, particularly snowstorms. In both years with significant snowfall in October, radioed deer moved rapidly and in a pulsed fashion from summer ranges to the winter range (Fig. 3). In a year without significant fall storms, movement was gradual, and males migrated significantly later than females. Previous studies discussed the relationship of snowstorms to fall migration (Russell 1932, Dixon 1934, Leopold et al. 1951, Richens 1967, Gilbert et al. 1970), although some cases were based on anecdotal evidence. Bertram and Rempel (1977) stated that deer on the west slope of the Sierra Nevada moved in anticipation of fall storms, but I found no evidence of this. Garrott et al. (1987) speculated that in northwest Colorado deer moved not because of snow, but to maximize the quality of their diets prior to winter. Differences in details of deer migration apparent between my study and studies in the western Sierra Nevada and in northwest Colorado indicate that deer migration can be influenced by local conditions.

Females may be constrained in their timing of fall migration by the nutritional and energetic demands of lactation and smaller body size, by the inability of fawns to cope with severe fall conditions, or both. Males do not have the same energetic, nutritional, or parental constraints. Additionally, as consequence of hunting regulations, those males that do migrate early are likely to be killed.

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DIATOM FLORA OF BEAVER DAM CREEK, WASHINGTON COUNTY, UTAH, USA

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ABSTRACT—The diatom flora of Beaver Dam Creek, Washington County, Utah, was studied. The study area is in a warm Mojave Desert environment at an elevation between 810 and 850 m. A total of 99 taxa were identified from composite samples taken in the fall, winter, spring, and summer seasons. These taxa are all broadly distributed and no endemic species were encountered. Three new records for the state of Utah were identified: *Gomphoneis eriense* Skv. & Mayer, *Navicula elginensis* var. *lata* (M. Perag.) Patr., and *Nitzschia calida* Grun. The most important taxa throughout the study as determined by multiplying percent presence by average relative density (Important Species Index) were *Cymbella affinis* Kütz., *Epithemia sorex* Kütz., *Navicula veneta* Kütz., *Nitzschia palea* (Kütz.) W. Sm., and *Nitzschia microcephala* Grun.

Key words: Beaver Dam Creek, diatoms, desert streams.

The algal flora of the Intermountain West of North America is not well known despite the fact that numerous studies dealing with algal systems of waters in this region have been completed in recent years. These studies have examined streams, fresh water lakes, saline lakes, thermal springs, and terrestrial habitats (Sommerfeld et al. 1975, Stewart and Blinn 1976, Czarnecki and Blinn 1977, 1978, Blinn et al. 1980, Bush and Fisher 1981; for bibliographies see Rushforth and Merkley 1988, Metting 1991).

Algal floras of warm desert systems are especially poorly known. The present study was initiated to provide additional information on the diatom flora of a desert stream located in western North America. We examined the diatom communities of Beaver Dam Creek, a tributary of the Virgin River in southwestern Utah. This paper is intended as a baseline floristic and community study of the diatom communities present in this Mojave Desert stream.

We had three objectives in this study: (1) to identify all species of diatoms present in Beaver Dam Creek, (2) to document seasonal variation in the diatom communities of this stream, and (3) to compare diatom populations according to habitat type. Our study reports all diatom taxa present in this stream across four seasons of 1987–88. We studied populations in (1) riffle areas with erosional flow velocities, (2) depositional areas with slower flows, and (3) epiphytic habitats on the stems and leaves of aquatic vascular plant vegetation.

SITE DESCRIPTION

Beaver Dam Creek at Lytle Ranch Preserve is located 37°10′ North latitude and 114° West longitude in Washington County, Utah (Fig. 1). The stream occurs in our study area at an elevation of about 850 m at Lytle Ranch dropping to 810 m at Terry's Ranch. Our study sites are located along the wash near the ranch house at Lytle Ranch Preserve and near a smaller outbuilding at Terry's Ranch.

Beaver Dam Creek is a vigorous, braided perennial desert stream. It is important to the entire biota of the area since it is the main source of perennial water. The stream through the study area has formed a broad gravel flood plain due to frequent flooding. The stream occurs in bajada and alluvial fan materials derived from the Bull Valley, Pine Valley, and Santa Clara mountains (Welsh et al. 1987).

Beaver Dam Creek is fed by seeps, springs, and snowmelt primarily from the Pine Valley Mountains. This area is also characterized by flash floods caused by severe periodic thunderstorms in the summer and fall seasons. For instance, prior to the April 1988 collection, Beaver Dam Wash received 11 days of rain

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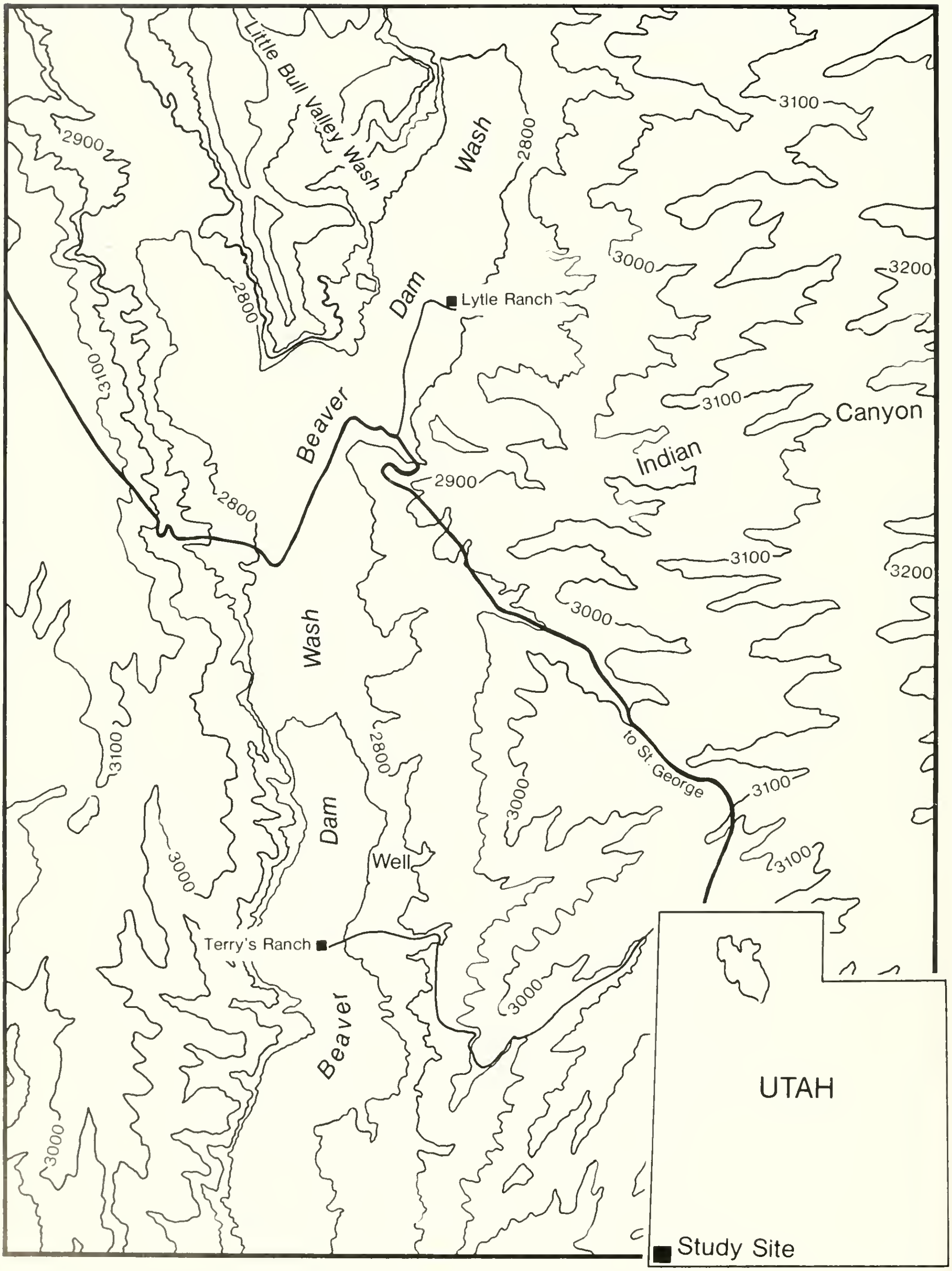
Little Bull Valley Wash
Beaver Dam Wash
Lytle Ranch
Indian Canyon
Wash
Dam
Beaver
Well
Terry's Ranch
to St. George
2800
2900
3000
3100
3200
UTAH
Study Site

Fig. 1. Map of Beaver Dam Wash showing the location of collecting localities at Terry's Ranch and Lytle Ranch Preserve. Due to the meandering and changing nature of Beaver Dam Creek, the stream itself is not shown on this map.

producing moderate to severe flooding along the stream channel. This scoured the stream channel, removing large amounts of aquatic vegetation and causing channel relocation in some areas.

The gravel bar in Beaver Dam Creek is generally higher in the center than at the margins, causing the stream to meander over a wide area with frequent changes of channel during flooding (Welsh et al. 1987). The fall in elevation downstream is not constant. Gravel tends to pile up in steps that vary in length and height. This uneven granular substrate causes the stream to meander along the gravel bar and eventually to sink underground approximately four miles below the southernmost collection site (Welsh et al. 1987). The perennial stream reappears infrequently as seeps and springs lower in Beaver Dam Wash until merging with the Virgin River.

Climate in the study area varies considerably, not only diurnally and seasonally, but over longer periods of time. Winters are generally cool and dry, summers hot and dry. Maximum summertime temperatures have been recorded at 45.6 C. Rainfall averages less than 15 cm a year, although this is variable due to intense storms (Welsh et al. 1987).

The biota of our study area is exceptionally diverse. Mammals, birds, reptiles, amphibians, invertebrates, and a great variety of plants occur in Beaver Dam Wash (Welsh et al. 1987). The stream supports a diverse riparian habitat consisting of Fremont cottonwood (*Populus fremontii* Wats.), Arizona ash (*Fraxinus velutina* Torr.), black willow (*Salix gooddingii* Ball), seep willow (*Baccharis emoryi* Gray *in* Torr.), numerous forbes, grasses, and grasslike species (Welsh et al. 1987). Silty terraces occur immediately adjacent to the wash and have been historically used for cultivation. These areas are dominated by catclaw acacia (*Acacia greggii* Gray), paniculate rabbitbrush (*Chrysothamnus paniculatus* [Gray] Greene), *Ambrosia* species, and numerous others (Welsh et al. 1987). Adjacent uplands support Joshua tree forests (*Yucca brevifolia* Engelm.), creosote bush (*Larrea tridentata* [DC.] Cov.), prickly pear cactus (*Opuntia engelmannii* Engelm.), cholla cactus (*Opuntia basilaris* Engelm. and Bigel.), and numerous other xerophytic species (Welsh et al. 1987).

METHODS

Water chemistry was sampled at the collection sites for February, April, and July 1988 using a portable Hach field water chemistry lab. Air temperature and water temperature, dissolved oxygen, hardness, alkalinity, and pH were measured.

Diatom collections were taken on 21 November 1987, 20 February 1988, 30 April 1988, and 6 July 1988 to document seasonal variations in diatom populations. Composite samples were collected from three habitat types. First, riffle areas with erosional flow rates were sampled by scraping algae from large stones in the creek bed. Second, slow water areas in the stream were sampled by obtaining sediments, rock scrapings, and visible attached algae. Finally, submerged sedge stems and leaves were scraped or collected at selected localities to study epiphytic assemblages.

Due to seasonal changes, it was not always possible to sample all three substrate types at both locations. A total of 19 samples were analyzed during the course of the study. Samples were stored at air temperature and returned to the laboratory at Brigham Young University for analysis.

Diatoms were cleared by boiling in nitric acid and potassium dichromate (St. Clair and Rushforth 1977). After rinsing, cleared frustules were suspended in distilled water and allowed to air dry on cover slips. Strewn mounts were prepared using Naphrax high-resolution resin. Representative slides were examined with Zeiss RA microscopes equipped with Nomarski optics and bright field illumination. An Olympus AD photomicrographic system was used to record each taxon. Strewn mounts have been placed in the collections at Brigham Young University.

A minimum of 500 valves was counted for each sample, and a percent relative density was calculated for each taxon (Kaczmarska and Rushforth 1983). An Important Species Index (ISI) for taxa present was calculated by multiplying the percent frequency of occurrence of a taxon in the samples by its overall average percent relative density in all samples (Ross and Rushforth 1980, Kaczmarska and Rushforth 1983). This method is useful since it considers both abundance and seasonal distribution of a taxon (Warner and Harper 1972). Species diversity for each sample was calculated using the

TABLE 1. Mean values for air temperature and water chemical parameters taken from collecting localities in Beaver Dam Creek, Washington County, Utah.

	February		April		July	
	Lytle	Terry's	Lytle	Terry's	Lytle	Terry's
Air temp. (C)	16.3	17.3	20.5	20.5	33.0	26.0
Water temp. (C)	14.5	17.5	16.8	16.8	24.3	22.3
Dissolved O_2 (mg/l)	9.5	10.0	9.0	9.0	7.7	7.0
Hardness (mg/l)	247.3	276.1	707.5	707.5	281.9	362.4
Alkalinity (mg/l	195.6	207.1			201.3	224.3
pH	7.3	7.1	6.9	7.0	8.1	7.7

TABLE 2. Taxa present in samples collected from Beaver Dam Creek, 1987–88, listed with Important Species Index (ISI) values. When ISI is below 0.01, the species is listed as a trace (T).

Taxon	ISI	Lytle	Terry
Achnanthes affinis Grun.	1.92	1.8	2.6
Achnanthes exigua Grun.	0.03	0.1	0.1
Achnanthes lanceolata (Bréb.) Grun.	2.51	3.8	1.1
Achnanthes minutissima Kütz.	1.92	3.4	1.3
Amphora libyca Ehr.	0.10	0.4	0.1
Amphora pediculus (Kütz.) Grun.	1.76	2.5	1.1
Amphora veneta Kütz.	0.13	0.6	0.1
Caloneis bacillum (Grun.) Cl.	T		
Caloneis silicula (Ehr.) Cleve	T		
Cocconeis pediculus Ehr.	0.04	0.1	0.1
Cocconeis placentula var. *euglypta* (Ehr.) Cleve	1.07	3.1	0.8
Cocconeis placentula var. *lineata* (Ehr.) V.H.	1.22	1.4	1.1
Cyclostephanos invisitatus (H. & H.) Ther., Stoerm. & Hak.	T		
Cyclotella meneghiniana Kütz.	0.72	1.0	0.5
Cymbella affinis Kütz.	17.57	23.4	13.2
Cymbella mexicana (Ehr.) Cl.	T		
Cymbella microcephala Grun.	0.58	1.2	0.5
Cymbella silesiaca Bleisch	0.16	0.4	0.1
Cymbella tumida (Bréb. *ex* Kütz.) V.H.	T		
Denticula elegans Grun.	1.44	2.5	0.4
Denticula elegans f. *valida* Pedic.	T		
Diatoma vulgare Bory	0.84	1.7	0.5
Diatoma vulgare var. *breve* Grun.	0.11	0.5	0.1
Epithemia adnata var. *proboscidea* (Kütz.) Hend.	0.07	0.1	0.3
Epithemia sorex Kütz.	13.25	1.8	35.9
Epithemia turgida (Ehr.) Kütz.	T		
Fragilaria construens (Ehr.) Grun.	0.21	0.5	0.2
Fragilaria construens f. *venter* (Ehr.) Hust.	0.50	0.5	0.8
Fragilaria pinnata Ehr.	0.14	0.2	0.3
Fragilaria vaucheriae (Kütz.) Peters.	2.21	1.1	3.0
Gomphoneis eriense (Grun.) Skv. & Meyer	0.02	0.1	0.1
Gomphoneis olivacea (Horne.) Dawson	0.27	0.7	0.2
Gomphonema acuminatum Ehr.	T		
Gomphonema angustum Agardh	0.51	0.8	0.4
Gomphonema clavatum (Ehr.)	0.06	0.2	0.2
Gomphonema grunowii Patr.	0.08	0.3	0.2
Gomphonema parvulum (Kütz.) Kütz.	1.89	2.1	0.2
Gomphonema pseudoaugur L.-Bert.	1.32	1.6	1.5
Gomphonema truncatum Ehr.	T		
Gyrosigma nodulifernm (Grun.) G. West	T		
Hantzschia amphioxys (Ehr.) Grun.	T		
Melosira varians Ag.	0.06	0.3	0.1
Meridion circulare (Grev.) Ag.	T		
Navicula abiskoensis Hust.	T		
Navicula atomus var. *permitis* (Hust.) L.-Bert.	0.08	0.2	0.1
Navicula bacillum Ehr.	0.09	0.2	0.2

TABLE 2. Continued.

Navicula capitatoradiata Germain	1.99	2.7	2.0
Navicula cincta (Ehr.) Ralfs	0.17	0.5	0.1
Navicula constans var. *symmetrica* Hust.	T		
Navicula cuspidata Kütz.	T		
Navicula elginensis var. *lata* (M. Perag.) Patr.	0.06	0.2	0.1
Navicula gregaria Donkin	0.16	0.5	0.1
Navicula menisculus Schumann	T		
Navicula minuscula var. *muralis* (Grun.) L.-Bert	0.06	0.3	0.1
Navicula pupula Kütz.	0.16	0.4	0.2
Navicula radiosa Kütz.	0.19	0.3	0.3
Navicula tripunctata (O.F. Müll.) Bory	0.12	0.5	0.1
Navicula tripunctata var. *schizonemoides* (V.H.) Patr.	0.10	0.4	0.1
Navicula trivialis L.-Bert.	0.28	0.6	0.2
Navicula veneta Kütz.	8.78	9.0	8.6
Neidium affine (Ehr.) Pfitz.	T	0.1	
Neidium dubium (Ehr.) Cl.	T		
Nitzschia acicularis (Kütz.) W.Sm.	0.02	0.1	0.1
Nitzschia amphibia Grun.	1.51	2.4	0.4
Nitzschia calida Grun.	0.02	2.0	
Nitzschia communis Rabh.	0.30	0.9	5.9
Nitzschia constricta (Kütz.) Ralfs	0.19	0.4	0.3
Nitzschia dissipata (Kütz.) Grun.	1.90	3.9	0.4
Nitzschia fonticola Grun.	0.58	1.1	0.4
Nitzschia frustulum (Kütz.) Grun.	0.01	0.1	
Nitzschia hantzschiana Rabh.	0.20	0.2	0.1
Nitzschia inconspicua Grun.	0.65	1.4	0.2
Nitzschia linearis (Ag.) W. Sm.	T		
Nitzschia microcephala Grun.	5.44	4.7	6.3
Nitzschia palea (Kütz.) W. Sm.	5.76	8.7	2.4
Nitzschia sigmoidea (Nitz.) W. Sm.	0.01	0.1	0.1
Nitzschia subtilis Grun.	T		
Pinnularia appendiculata (Ag.) Cl.	T	0.1	
Pleurosigma delicatulum W. Sm.	0.02		0.2
Pleurosira laevis (Ehr.) Compere	T		
Reimeria sinuata (Greg.) Kociolek & Stoermer	T	0.1	
Rhoicosphenia curvata (Kütz.) Grun.	2.73	1.4	4.9
Rhopalodia brebissonii Krammer	T		
Rhopalodia gibba (Ehr.) O. Müll.	T		
Rhopalodia gibba var. *ventricosa* (Kütz.) Perag. & Perag.	0.01	0.1	
Rhopalodia gibberula (Ehr.) O. Müll.	0.03	0.2	0.1
Stauroneis smithii Grun.	T	0.1	
Stenopterobia intermedia (Lewis) V.H.	T		
Stephanodiscus hantzschii Grun.	0.02		0.1
Surirella angusta Kütz.	0.06	0.2	0.1
Surirella minuta Bréb.	T		
Surirella ovalis Bréb.	T		
Synedra acus Kütz.	T		
Synedra fasciculata var. *truncata* (Grev.) Patr.	T		
Synedra radians Kütz.	0.01	0.1	0.1
Synedra rumpens var. *meneghiniana* Grun.	0.11	0.1	0.3
Synedra ulna (Nitz.) Ehr.	0.40	0.7	0.5
Synedra ulna var. *contracta* Oestr.	0.20	0.3	0.3

Shannon-Wiener diversity index (Shannon and Weaver 1949, Zar 1986).

Similarity indices were calculated for all pairs of samples following Ruzicka (1958). Cluster analyses based on Ruzicka's indices using unweighted pair-group techniques (UPGMA) were then performed (Sneath and Sokal 1973). This method computes the average similarity of each site to every other site using arithmetic averages. It is widely used and has been found to introduce less distortion than other methods (Kaesler and Cairns 1972).

RESULTS AND DISCUSSION

Water chemistry did not vary significantly according to collection locality (Table 1). Stream temperature increased somewhat during the summer months, but it is noteworthy that temperature variations in the stream were relatively small. The stream is circumneutral to slightly alkaline.

A total of 99 diatom taxa in 24 genera were observed in our collections. Three new records for the state of Utah were noted: *Gomphoneis eriense* (Grun.) Skv. & Meyer, *Navicula elginensis* var. *lata* (M. Perag.) Patr., and *Nitzschia calida* Grun. Taxa are illustrated and described in Yearsley (1988). Nomenclature followed in Yearsley (1988) was similar to that used historically by researchers in our laboratory for comparative purposes (Rushforth and Merkley 1988). Diatom taxonomy in this paper is based primarily on the recent texts of Krammer and Lange-Bertalot (1986, 1988, 1991), although other references were consulted and sometimes followed. We did not follow the numerous generic changes proposed in Round et al. (1990) due to the controversy over many of their recommendations.

Eighteen taxa in Beaver Dam Creek had an Important Species Index value greater than 1.0 (Table 2). The most important taxa in the overall study with ISIs above 5.0 were *Cymbella affinis* (ISI = 17.57), *Epithemia sorex* (13.25), *Navicula veneta* (8.78), *Nitzschia palea* (5.76), and *Nitzschia microcephala* (5.44). Taxa with ISIs greater than 1.0 included *Rhoicosphenia curvata* (2.73), *Achnanthes lanceolata* (2.51), *Fragilaria vaucheriae* (2.21), *Navicula capitatoradiata* (1.99), *Achnanthes affinis* (1.92), *Achnanthes minutissima* (1.92), *Nitzschia dissipata* (1.90), *Gomphonema parvulum* (1.89), *Nitzschia amphibia* (1.51), *Denticula elegans* (1.44), *Gomphonema pseudoaugur* (1.32), *Cocconeis placentula* var. *lineata* (1.22), and *Cocconeis placentula* var. *euglypta* (1.07). All of these taxa are cosmopolitan and found in a variety of habitats.

In comparing the diatom assemblage from Beaver Dam Creek with the floras of streams of other arid regions, we noticed a striking similarity. The important taxa overlapped in all of the studies even though the streams varied in terms of their flow rate and climatic regime. Furthermore, each system was dominated by cosmopolitan species. Our preliminary data indicate that a diatom flora unique to desert streams does not exist. Further research to substantiate this conclusion is necessary; some evidence is given below.

Blinn et al. (1980) considered substrate colonization in Oak Creek, Arizona. They reported 12 important taxa which, in order of decreasing abundance, were: *Nitzschia frustulum, Epithemia sorex, Cocconeis placentula* var. *euglypta, Achnanthes minutissima, Navicula cryptocephala, Navicula veneta* (as *N. cryptocephala* var. *veneta*), *Nitzschia dissipata, Achnanthes lanceolata, Cymbella affinis, Fragilaria construens, Navicula decussis,* and *Synedra ulna.* These diatoms accounted for 90% or more of the total algal population on newly introduced material in their study. Eight of these taxa were also important in our stream, having ISI values above 1.0.

Johnson et al. (1975) conducted further study on the diatom flora of Oak Creek, Arizona. They reported 41 diatom taxa, of which 25 are common to our study area. *Cymbella affinis, Epithemia sorex,* and *Nitzschia palea* were reported as common or abundant. This compares favorably with the results of our study since these three were among the most common diatoms in Beaver Dam Creek.

Rushforth et al. (1976) examined the algal flora of Freshwater Wash, Arches National Park, in southeastern Utah. Their study documented 57 diatom taxa, 29 of which were also observed in Beaver Dam Creek. *Achnanthes minutissima, Cymbella affinis, Denticula elegans, Gomphonema acuminatum, Navicula radiosa, Nitzschia linearis, Nitzschia palea, Rhoicosphenia curvata,* and five other species not present in Beaver Dam Creek were the most abundant taxa in Freshwater Wash.

In their analysis of Sycamore Creek, Arizona, Fisher et al. (1982) reported that diatoms made up 77% of the total algal mass, with *Achnanthes exigua, Gomphonema parvulum,* and *Navicula pupula* being the most important taxa. These taxa were present in Beaver Dam Creek but in lower numbers. *Gomphonema parvulum* was the most abundant of the three in our samples.

The flora of Beaver Dam Creek is also similar to that of other streams of western North America draining more mesic regions. Cushing and Rushforth (1984) in a study of the Salmon River, Idaho, identified 145 diatom species, 48 of which were among the 99 taxa found in Beaver Dam Creek. Half of their important species (9 of 18) were also among the important species in Beaver Dam Creek, several with similar importance values.

Preliminary research also indicates that a flora similar to that found in North American hardwater streams exists elsewhere. Squires and Saoud (1986) reported nine taxa from the Damour River, Lebanon, with Importance Species Index values above 1.0. Six of these also were important in Beaver Dam Creek. In the Damour River study *Achnanthes minutissima* was the most important taxon with an ISI value of 44.4, followed by *Nitzschia dissipata* (5.12), *Cymbella microcephala* (3.63), and *Cymbella affinis* (2.62).

Shannon-Wiener diversity values for all 24 samples ranged between 1.95 and 4.59. Diversity did not show any clear trends with regard to season or substrate type. The overall mean for the indices was 3.42, the median value being 3.57. These values are relatively high and indicative of unpolluted water.

Our collections did not cluster well on the basis of habitat type or season. However, there was a tendency for stands to cluster on the basis of the Terry's Ranch versus Lytle Ranch Preserve collecting localities (Fig. 2). The uppermost cluster consists of samples from Terry's Ranch, while the second cluster contains samples from the Lytle Ranch Preserve. The third cluster has a mix of all sites, substrates, and seasons. The fall depositional sample from the Lytle Ranch Preserve is an outlier.

The reasons for the clustering by site seen in the top half of the cluster are unclear. Water chemistry and temperature did not vary greatly between the sites during the year (Table 1). Likewise, insolation is approximately the same for both sections of the creek. Stream velocities, however, appear to be different. The creek at Lytle Ranch Preserve is generally slower, shallower (<15 cm), wider, and more meandering than the stream at Terry's Ranch where pools may reach depths of nearly one meter.

The cluster shows a number of samples that paired by date of collection (Fig. 2). However, seasonality was very weak. The absence of seasonal changes is probably attributable to one or two factors. First, temperature changes throughout the year are minor, and changes in photoperiod alone are not enough to drive succession. Second, storm events scour the creek bed occasionally and may keep the diatom assemblage in an early successional stage.

The habitat types sampled did not cluster separately, indicating they are fairly similar. Because of scouring events, the depositional areas initially sampled often had all sediments removed at later sampling dates and so consist of rock scrapings, just as in the riffle areas. The one sample that consisted of sediment only (Lytle Ranch, November 1987, depositional area) clustered separately from all other samples (see bottom line of cluster, Fig. 2).

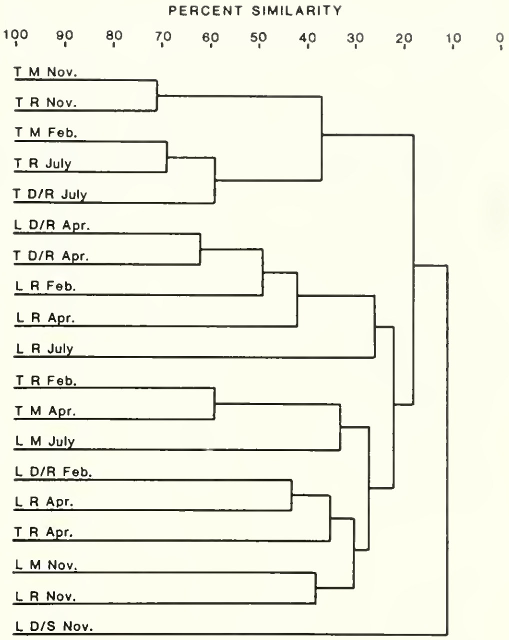

Fig. 2. Cluster diagram of 19 samples collected from Beaver Dam Creek. T = Terry's Ranch, L = Lytle's Ranch Preserve, M = macrophytic vegetation (sedges), R = riffle, D/S = depositional area, sediments, D/R = depositional area, rock scrapings.

In summary, the diatom assemblages observed in Beaver Dam Creek consisted of cosmopolitan species common to other hardwater rivers. Seasonality was minimal, as were the effects of habitat type.

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STRATIFICATION OF HABITATS FOR IDENTIFYING HABITAT SELECTION BY MERRIAM'S TURKEYS

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ABSTRACT.—Habitat selection patterns of Merriam's Turkeys were compared in hierarchical analyses of three levels of habitat stratification. Habitat descriptions in first-level analyses were based on dominant species of vegetation. Habitat descriptions in second-level analyses were based on dominant species of vegetation and overstory canopy cover. Habitat descriptions in third-level analyses were based on dominant species of vegetation, overstory canopy cover, and structural stages (dbh categories). First-level analyses showed turkeys selected for ponderosa pine and selected against meadow habitats. No conclusions could be drawn regarding forest management on habitat selection of turkeys at this level of habitat stratification. Second-level analyses showed that selection of ponderosa pine and aspen/birch habitats varied among seasons. Implications for forest management activities on turkeys at this level of habitat stratification could be made. Third-level analyses added little to conclusions of habitat selection patterns drawn from second-level analyses and increased chances for Type II errors. Habitat selection patterns of Merriam's Turkeys were best described when habitats were stratified by dominant species of vegetation and overstory canopy cover.

Key words: Merriam's Wild Turkeys, Meleagris gallopavo merriami, *habitat descriptions, forest management, habitat selection.*

Habitat use and management of Merriam's Turkeys (*Meleagris gallopavo merriami*) in northern latitudes have been studied in South Dakota (Petersen and Richardson 1975) and Montana (Rose 1956, Jonas 1966). These early studies were limited to direct observation of birds when assessing habitat use, and data contained biases in the assessment of the birds' habitat needs (e.g., Jonas 1966, Bryant and Nish 1975, Petersen and Richardson 1975, Shaw and Smith 1977). Telemetry has allowed collection of data on habitat use patterns in an unbiased manner, but few studies have addressed the detailed stratification habitats.

Studies of habitat use and selection patterns by Merriam's Turkeys have delineated habitats based primarily on the dominant species of vegetation (DSV) (Jonas 1966, Bryant and Nish 1975, Scott and Boeker 1975, Mackey 1982, 1986, Lutz and Crawford 1989). Because timber management activities seldom result in conversions of vegetation types, understanding habitat selection patterns at this level precludes understanding the effects of forest management activities such as logging or thinning on Merriam's Turkeys. Increased value of ponderosa pine timber resources, emphasis on old-growth resource values, and improved technology for harvesting timber have potential to impact Merriam's Turkey habitat (Shaw 1986). Therefore, stratification beyond dominant species of vegetation is necessary to elucidate the effects of forest management on turkeys. Merriam's Turkeys in southeastern Montana demonstrated an apparent preference for pole-size (<23 cm dbh) ponderosa pine habitats (Jonas 1966). Merriam's Turkeys in Oregon avoided habitats that had been logged by clear-cut or shelterwood methods (Lutz and Crawford 1989). To our knowledge, no researchers have stratified habitats in terms of size and density categories of tree species. However, on lands managed by the USDA Forest Service and other public agencies, methods of habitat stratification that include structural stages (SS) and overstory canopy cover categories (OCC) have been described (Thomas 1979) to further stratify habitats.

The objective of this study was to determine the level of habitat stratification that best described habitat use and selection patterns of Merriam's Turkeys in the Black Hills.

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METHODS

Study Area

This study was conducted in the central Black Hills of South Dakota, 16 km west of Rapid City. Most of the land is under management by the Black Hills National Forest, Pactola Ranger District. Some private holdings associated with ranch operations are present in the meadows, and several private homes and cabins are located in the study area.

Vegetation of the study area is primarily pure ponderosa pine forest (84%). Meadows and aspen/birch (*Populus tremuloides/Betula papyrifera*) habitats occur in drainages.

This study was conducted over a three-year period beginning March 1986 and ending January 1989. Because analytical methods used to make statistical tests were goodness-of-fit tests and nonsignificance indicates fit by the proposed model, hypotheses tested have been stated appropriately. The hypotheses tested relative to Merriam's Turkeys in the Black Hills of South Dakota were that each of the following habitats depict patterns of use and selection by Merriam's Turkeys: (1) habitats stratified by DSV, (2) habitats stratified by DSV and OCC, (3) habitats stratified by DSV and SS, and (4) habitats stratified by DSV, SS, and OCC.

TRAPPING AND LOCATIONS.—Turkeys were trapped in late February or early March of each year of the study with rocket nets and drop nets over corn bait. This study was primarily concerned with hens since they are the reproductive segment of the population. Forty-four (36 females and 8 males) of 82 turkeys trapped were fitted with backpack radio transmitters weighing approximately 108 g.

Locating birds began after a one-week period of adjustment to the radio transmitters (Nenno and Healy 1979). Each bird in the study area was located three times each week, once during each of the following time periods: sunrise–1000 hr, 1001–1400 hr, and 1401 hr–sunset. Birds that emigrated from the defined study area were located at least monthly to monitor their activities and determine if they had moved back into the study area. Locations were determined by plotting 2+ bearings (frequently 5+) from known locations on USGS 1:24,000 contour maps in the field using a hand-held, two-element yagi antenna. Bearings were usually taken from positions within 300 m of the estimated location. Each location was assigned to a habitat unit (see below) based on maps and Universal Transverse Mercator coordinates recorded to the nearest 100 m in the field. To achieve independence of observations (Alldredge and Ratti 1986), only one location was recorded for each bird on any given day and most were two days apart.

Habitat Descriptions

Habitats were numerically identified geographical units approximately 4–32 ha (10–80 acres) in size. Boundaries were usually defined by watershed topography such as ridges and drainages. Obvious changes in vegetation type also were used to define boundaries of habitats. In all, 513 habitat units were delineated.

Vegetative descriptions of habitats were determined from five plots located within each defined habitat unit. These plots were marked on unit 1:24,000 contour maps in the lab and distributed evenly across each habitat. Some habitats were too small to effectively place five plots, so fewer plots were used. Each plot was then located in the field and sampled to determine tree basal area.

Habitat descriptions were made based on DSV, SS, and OCC according to criteria developed by the USDA Forest Service, Region 2 (Buttery and Gillam 1983). DSV categories were ponderosa pine, aspen/birch, oak, spruce, and meadows. SS categories were pole timber (trees 2.5–22.8 cm dbh) and sawtimber (trees greater than 22.8 cm dbh). OCC categories were 0–40%, 41–70%, and 71–100%. OCC was estimated based on the following equation: OCC(%) = 0.51*BASAL AREA (FT^2/AC) − 1.94 (Bennett 1984). Depending on the level of stratification included in the analyses, 5–12 habitats were delineated.

Analyses

Data pertaining to use of habitats described above were stratified into seasons: December–February (winter), March–May (spring), June–August (summer), and September–November (fall). Chi-square test of independence was used to test the hypothesis that habitat use patterns of Merriam's Turkeys were similar among seasons. Because this test was significant ($P < .001$), tests of habitat selection at different levels of habitat stratification were made within seasons.

Chi-square goodness-of-fit tests with correction for continuity (Cochran 1963) were used to test hypotheses regarding the level of habitat stratification that best depicted habitat selection patterns of Merriam's Turkeys in a hierarchical structure. Bonferroni confidence intervals around proportion of use (Neu et al. 1974, Byers et al. 1984) were used to determine habitat selection patterns that deviated from expected use. We determined differences from expected use of habitats for which utilization was 0 by examining chi-square residuals with G-standardization and Bonferroni correction to the Z-statistic (Mosteller and Parunak 1985). An array of structural stages occurred only for ponderosa pine habitats. Therefore, the test for DSV × SS level of habitat stratification was analyzed using data from ponderosa pine habitats.

Initial chi-square tests of use versus availability for DSV × SS, DSV × OCC, and DSV × SS × OCC were made with oak, aspen, and spruce habitats pooled to reduce as much as possible the number of cells with fewer than five expected observations. Selection of these habitats by turkeys was evaluated individually with Bonferroni confidence intervals for comparison tests. The significance of confidence intervals holds regardless of the overall chi-square test (Neu et al. 1974).

RESULTS

Habitats Determined by DSV

The hypothesis that habitats stratified by DSV depict patterns of habitat use and selection by Merriam's Turkeys was rejected ($P = .06$). Meadows were selected less than expected across all seasons (Table 1). Ponderosa pine habitats were selected more than expected during winter, spring, and fall; they were equal to what was expected during summer. Aspen habitats were selected more than expected during summer. Oak habitats were selected less than expected during spring, while spruce habitats were selected less than expected during winter and spring.

Habitats Determined by DSV and OCC

The hypothesis that habitats stratified by DSV and OCC depict patterns of habitat use and selection by Merriam's Turkeys was rejected for all seasons ($P = .04$). Stratifying habitats by DSV and OCC did not alter the results for meadow, oak, or spruce habitats (Table 2). Oak and spruce were not represented across all overstory canopy cover categories on this study area.

Aspen/birch habitats with 41–70% OCC were selected more than expected during spring and summer by turkeys in the Black Hills. Infrequent use of aspen/birch habitats with 71–100% OCC was noted over all seasons. But statistically, this was less than expected only during spring. Open ponderosa pine habitats (0–40% OCC) were selected less than expected during the winter and spring. Turkeys selected ponderosa pine habitats 41–70% OCC more than expected during spring. Dense ponderosa pine habitats (71–100% OCC) were selected more than expected during fall and winter and less than expected during summer.

Habitats Determined by DSV and SS

The hypothesis that habitats stratified by DSV and SS depicted patterns of habitat use and selection by Merriam's Turkeys was not rejected for winter, summer, and fall. During spring, ponderosa pine habitats with stems greater than 23 cm dbh were selected more than expected. Otherwise, no differences were apparent in the habitat selection patterns of turkeys when pine habitats were stratified based on dbh. Aspen/birch, oak, and spruce habitats were not adequately represented across structural stages to make comparisons.

Habitats Determined by DSV, SS, and OCC

The hypothesis that habitats stratified by DSV, SS, and OCC depict patterns of habitat use and selection by turkeys was rejected ($P = .03$) during winter, spring, and summer (Table 3). Data from fall indicated observed differences from expected at $P = .11$. Since several habitat categories were pooled to achieve minimum sample size in the overall chi square test, $P = .11$ was considered sufficient indication of difference from expected to proceed with the Bonferroni confidence intervals.

Use patterns of meadow, oak, and spruce habitats by Merriam's Turkeys were unchanged from previous levels of habitat stratification. However, because more habitats were included in the analyses, selection of spruce during winter and aspen/birch habitats with 41–70% overstory canopy cover during summer no longer differed from expected.

Turkeys selected open ponderosa pine habitats in both structural stages less than expected during winter, and the 2.5–22.8 cm dbh structural

TABLE 1. Seasonal utilization by Merriam's Turkeys of habitats described by dominant species of vegetation in the Black Hills of South Dakota.[a,b]

Habitat	Proportional area	Winter (205)	Spring (878)	Summer (126)	Fall (218)
Aspen	0.0516	4—	61	17++	14
Meadow	0.1016	11—	9—	5—	7—
Pine	0.8371	186++	807++	100	195++
Oak	0.0044	4	0—	1	1
Spruce	0.0056	0—	1—	3	1

[a]Sample sizes (telemetry fixes) are in parentheses Expected use can be calculated from proportional use × sample size.
[b]Differences ($P \leq .10$) among habitats selected versus available are indicated by — if used less than expected and ++ if used more than expected

TABLE 2. Seasonal utilization by Merriam's Turkeys of habitats described by dominant species and overstory canopy cover of vegetation in the Black Hills of South Dakota.[a,b]

Habitat	Percent canopy cover	Proportional area	Winter (205)	Spring (878)	Summer (126)	Fall (218)
Aspen/birch	0–40	0.0148	2	14	4	1
Aspen/birch	41–70	0.0191	0	46++	11++	12
Aspen/birch	71–100	0.0177	2	1—	2	1
Ponderosa pine	0–40	0.1199	3—	63—	26	29
Ponderosa pine	41–70	0.3760	65	430++	45	71
Ponderosa pine	71–100	0.3412	118++	314	29—	95++
Meadows		0.1016	11—	9—	5—	7—
Oak	0–100	0.0044	4	0	1	1
Spruce	0–100	0.0056	0	1—	3	1

[a]Sample sizes (telemetry fixes) are in parentheses. Expected use can be calculated from proportional use × sample size.
[b]Differences ($P \leq .10$) among habitats selected versus available are indicated by — if used less than expected and ++ if used more than expected.

TABLE 3. Seasonal utilization by Merriam's Turkeys of habitats determined by dominant species, overstory canopy cover, and structural stage in the Black Hills of South Dakota.[a,b]

Habitat	Structural stage	Percent canopy cover	Proportional area	Winter (205)	Spring (878)	Summer (126)	Fall (218)
Aspen/birch	2.5–22.8 cm	0–40	0.0148	2	14	4	1
Aspen/birch	2.5–22.8 cm	41–70	0.0191	0	46++	11	12
Aspen/birch	2.5–22.8 cm	71–100	0.0177	2	1—	2	1
Ponderosa pine	2.5–22.8 cm	0–40	0.0701	1—	9—	20++	18
Ponderosa pine	2.5–22.8 cm	41–70	0.1677	32	143	25	33
Ponderosa pine	2.5–22.8 cm	71–100	0.2173	85++	222	16—	62
Ponderosa pine	>22.8 cm	0–40	0.0498	2—	54	6	11
Ponderosa pine	>22.8 cm	41–70	0.2083	33	287++	20	38
Ponderosa pine	>22.8 cm	71–100	0.1239	33	92	13	33
Meadows			0.1016	11—	9—	5—	7—
Oak		0–100	0.0044	4	0	1	1
Spruce		0–100	0.0056	0	1—	3	1

[a]Sample sizes (telemetry fixes) are in parentheses. Expected use can be calculated from proportional use × sample size.
[b]Differences ($P \leq .10$) among habitats selected versus available are indicated by — if used less than expected and ++ if used more than expected.

stage was selected less than expected during spring. No differences were noted for ponderosa pine with 41–70% overstory canopy cover and 2.5–22.8 cm dbh across seasons. However, the structural stage greater than 22.8 cm dbh and 41–70% overstory canopy cover was selected more than expected during spring. Dense ponderosa pine (>71% overstory canopy cover) 2.5–22.8 cm dbh was selected more than expected during winter and less than expected during summer. No differences were noted for dense ponderosa pine >22.8 cm dbh.

DISCUSSION

The highest level of stratification of habitats that added new information to use and selection patterns of Merriam's Turkeys in this study area was by DSV and OCC. Despite statistical significance of differences when habitats were stratified by DSV, SS, and OCC, trends in habitat selection were similar to analyses for which data were pooled across SS categories. Shaw and Smith (1977) noted apparent habitat selection by Merriam's Turkeys in Arizona when ponderosa pine habitats based on diameter classes were ignored. However, pole-size ponderosa pine habitats were used more than other size classes by turkeys in Montana (Jonas 1966). Within our study area, 12 of the 372 ponderosa pine habitats had an average dbh of less than 15 cm (6 in); the lowest average dbh was 10.7 cm (4.2 in). Thirty-seven of the ponderosa pine habitats in the study area had dbh greater than 30 cm (12 in), of which the majority were in the 0–40% OCC category indicative of large overmature trees. Most of the study area had been logged in the past one hundred years. Because excellent germination conditions for ponderosa pine in the Black Hills result in overstocked stands with reduced growth rates (Boldt and Van Duesen 1974), ponderosa pine habitats larger than 30 cm dbh were rare. Ponderosa pine habitats in this study were representative of a narrow range of the potential tree dbh classes for ponderosa pine. However, they did represent the size classes of ponderosa pine throughout the Black Hills.

The tests of the model for DSV × SS suggested good agreement between the model and observed use by turkeys from a statistical point of view. These results suggest random selection of habitats when stratified by DSV × SS. Nonrandom selection of habitats had already been demonstrated. We also believe that stratification of habitats by DSV × SS obscured biological patterns already demonstrated by the test of DSV × OCC. Many of the relationships of OCC were contrasted between high and low OCC. These results were pooled, resulting in the apparently good fit of the DSV × SS model.

Our approach to these analyses was hierarchical in nature; and since patterns of habitat selection by turkeys had been demonstrated at higher levels, it would not be prudent to ignore those biological patterns. However, to ensure that no oversights were made, we made tests of habitat selection based on habitats stratified by SS, OCC, and SS × OCC. The test of the model for SS was not rejected. Tests of the model for OCC and SS × OCC were rejected, but were influenced by the preponderance of the study occupied by ponderosa pine (84%) and the range of dbh classes in the Black Hills. Interpretations of results from these latter tests were similar to tests of DSV × SS and DSV × OCC.

Stratification of habitats beyond that necessary to depict the dispersion patterns of the animal decreases the sensitivity of tests and increases the probability of Type II error in the analyses (Alldredge and Ratti 1986). The effect of adding stratification factors is to dilute the sample sizes in individual cells, thus increasing the chance of Type II error. Apparent Type II errors occurred in the determination of habitat selection patterns when habitats were stratified by DSV × SS × OCC. At the highest level of habitat stratification, apparent differences from expected use for three habitat categories disappeared from the analyses.

ACKNOWLEDGMENTS

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POLLINATOR PREFERENCES FOR YELLOW, ORANGE, AND RED FLOWERS OF *MIMULUS VERBENACEUS* AND *M. CARDINALIS*

Robert K. Vickery, Jr.[1]

ABSTRACT.—Red, orange, and yellow morphs of *Mimulus verbenaceus* and *M. cardinalis* were field tested for pollinator preferences. The species are closely similar except that *M. verbenaceus* flowers have partially reflexed corolla lobes, whereas *M. cardinalis* flowers have fully reflexed corolla lobes. On the basis of over 6000 bumblebee and hummingbird visits, highly significant ($p < .001$) patterns emerged. Yellow, which is the mutant color morph in both species and is determined by a single pair of genes, was strongly preferred by bumblebees and strongly eskewed by hummingbirds in both species. Orange and, to a lesser extent, red were strongly preferred by hummingbirds but eskewed by bumblebees in both species. Thus, strong, but partial, reproductive isolation was observed between the yellow mutants and the orange- to red-flowered populations from which they were derived. Color—yellow versus orange and red—appeared more important than shape—partially reflexed versus fully reflexed corolla lobes—in determining the preferences of the guild of pollinators in this particular test environment for *Mimulus verbenaceus* and *M. cardinalis*.

Key words: Mimulus, *speciation, flower colors, pollinator preferences, bumblebees, hummingbirds.*

How much of a change in flower color and/or shape is enough to lead to a change in pollinators and hence to reproductive isolation and potentially to speciation? The flower color and shape morphs of *Mimulus verbenaceus* Greene and *M. cardinalis* Douglas provide an excellent system for addressing this intriguing question.

MATERIALS

Mimulus verbenaceus and *M. cardinalis* are typically bright red flowered and hummingbird pollinated. However, yellow-flowered morphs occur in *M. verbenaceus*, e.g., in a population at Vassey's Paradise, Grand Canyon, Arizona, and in *M. cardinalis* populations, e.g., on Cedros Island, Baja California, Mexico, and in the Siskyou Mountains, Oregon. My experimental hybridizations show that yellow is due to a single pair of recessive genes that limit the floral anthocyanins to small dots in the corolla throat. Intermediate, orange-flowered forms are known in *M. verbenaceus*, specifically the population at Yecora, Sonora, Mexico. And, an intermediate, orange-flowered form of *M. cardinalis* was obtained by repeated cycles of selection. In both cases orange is due to a single pair of quantitative genes that reduce the amount of anthocyanin pigments in the corolla lobes. Thus, parallel series of red, orange, and yellow color forms are available for both *M. verbenaceus* and *M. cardinalis* (Table 1).

Mimulus verbenaceus and *M. cardinalis* are similar, closely related species in section *Erythranthe* (Grant 1924); however, their flowers differ in shape. Those of *M. verbenaceus* have only the upper pair of corolla lobes sharply reflexed, giving the flowers a partially tubular aspect. The side pair of lobes and the labellum curve gently forward forming a bee landing platform. Flowers of *M. cardinalis* have both the upper and side corolla lobes sharply reflexed, giving the flowers a fully tubular shape. The labellum is thrust forward and is folded on itself forming a ridge instead of a landing platform. Shapes of the flowers of both species would seem to invite hummingbirds. Flowers of *M. verbenaceus* but not those of *M. cardinalis* would appear adapted for bees as well. However, flowers of all three color morphs of both species showed no reflectance patterns in the ultraviolet, that is, no putative bee nectar guides. Thus, flower shapes of *M. verbenaceus* and *M. cardinalis* are similar in some respects but differ in others of potential significance to pollinators.

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PLAN

The effect of flower color and flower shape on pollinator preferences will be addressed stepwise. First, pollinator preferences for color—red, orange, and yellow—will be ascertained for *M. verbenaceus* plants only, holding flower shape constant. Second, red-, orange-, and yellow-flowered *M. cardinalis* plants will be added to the experiment. Are pollinator preferences for red, orange, and yellow flowers of *M. cardinalis* the same as for those of the *M. verbenaceus* series? Note that the pigments are identical (Vickery 1978). Or, does the difference in corolla shape between the two species lead to a difference in pollinator preferences?

METHODS

Seeds for each of the six populations of the study (Table 1) were collected in the wild or harvested from transplants brought into the greenhouse except those of orange *M. cardinalis*, which were obtained by selection. A large population of red *M. cardinalis* from Cedros Island was grown and the most orange-red flowered plant self-pollinated. Its progeny included several orange-flowered plants. Progeny of these plants were grown and found to breed true for orange and were used as the source of seeds for the orange *M. cardinalis* morph.

Seeds of the six populations were sown in early April 1988 in the University of Utah greenhouse, following which seedlings were transplanted into 4" plastic pots and grown to flowering. Pots were placed in plastic trays to facilitate bottom-watering, plants being randomly arranged as to flower color.

When plants began flowering, they were moved outdoors to test pollinator preferences. Instead of using Red Butte Canyon Natural Research Area as before (Vickery 1990), with its relative paucity of pollinators, I scattered the plants on a lawn adjacent to native gambel oak clumps at the mouth of Parley's Canyon of the Wasatch Mountains in an area rich in pollinators. Some 50 to 100 plants of each color morph of *M. verbenaceus* made up the artificial population of the first part of the experiment. Some 50 to 100 plants of red and of orange *M. cardinalis* plus 20 plants of yellow *M. cardinalis* (all that were available) were added to the *M. verbenaceus* plants for the second part of the experiment.

TABLE 1. Origin of populations studied.

***Mimulus verbenaceus* Greene**
Vassey's Paradise, Grand Canyon, Arizona, USA, elev. ~650 m
Red morph = culture number 14,088
Yellow morph = culture number 14,089
Yecora, Sonora, Mexico, elev. ~1,550 m
Orange = culture number 13,256

***Mimulus cardinalis* Douglas**
Isla Cedros, Baja California, Mexico, elev. ~100 m
Red morph = culture number 13,106
Yellow morph = culture number 13,250
Orange = culture number 13,249
(obtained by selection from the red morph)

Pollinator visits to the flowers were observed and recorded for an average of 1½ hours per observation period for 15 periods for each of the two parts of the experiment (Tables 2, 3). Time of day of the observations was varied to be sure of noting all the different kinds of visitors. To count as a visit, a hummingbird had to thrust its beak into a flower. A bee had to land on the flower and crawl into the flower far enough to brush the stigma and anthers. A fly, butterfly, etc., had to walk on the reproductive structures. The numbers of flowers rather than plants of each color of each species were recorded for each observation period.

For analysis of visits, chi-square tests were run for each observation period for each part of the experiment. The null hypothesis was that hummingbirds or bumblebees (very few flies, butterflies, etc., visited the flowers and were not listed) would visit the three colors of flowers of *M. verbenaceus* in the first part of the experiment and the three colors of *M. verbenaceus* and *M. cardinalis* in the second part of the experiment in proportion to the numbers of those flowers in the experimental population (Tables 2, 3). If the overall chi-square value for a period of, for example, bee visits to *M. verbenaceus* or hummingbird visits to *M. cardinalis* indicated a significant deviation from expected values, then the frequency of visits to each color was inspected. Those high or low enough that their term in the chi-square equation was large enough by itself to produce a significant deviation at the 5% level were considered to be significant (Tables 2, 3).

TABLE 2. Pollinator preferences for red, orange, or yellow flowers of *Mimulus verbenaceus* in 1988.

	Numbers of flowers			Bumblebee visits				Hummingbird visits			
Month:day:time	Red	Orange	Yellow	Red	Orange	Yellow	P	Red	Orange	Yellow	P
7:26:1630	48	56	70	28↓[a]	523↑	198↓	<.001	0	3	0	<.100
7:29:0745	56	91	74	30	50	58	<.200	0	81↑	29	<.010
7:30:0710	46	79	114	24	67	67	<.010	55↑	66	70	<.010
8:02:1640	85	77	74	3↓	88↑	53	<.001	27	49	27	<.010
8:03:0630	92	101	133	53	99↑	81	<.001	33	79↑	36↓	<.001
8:03:1540	120	117	172	31↓	74	209↑	<.001	100↓	241↑	183	<.001
8:04:0640	86	73	178	0↓	5	52↑	<.001	83	145↑	170	<.001
8:05:0715	120	100	169	33↓	71	125	<.001	9↓	77↑	28↓	<.001
8:05:1645	126	104	174	12↓	22↓	126↑	<.001	36↓	149↑	92↓	<.001
8:05:1830	126	104	174	5↓	4↓	73↑	<.001	75	150↑	82↓	<.001
8:06:0840	126	88	151	74↓	159↑	291↑	<.001	66	100↑	26↓	<.001
8:06:1445	126	98	150	6↓	6↓	60↑	<.001	49	94↑	24↓	<.001
8:06:1810	130	117	142	50	105	257↑	<.001	31	48↑	1↓	<.001
8:07:1515	130	119	142	0↓	4↓	68↑	<.001	52	125↑	5↓	<.001
8:08:0725	118	91	124	12↓	32	131↑	<.001	32	67↑	5↓	<.001

[a] ↑ or ↓ = significantly high or low; see text

TABLE 3. Pollinator preferences for red, orange, or yellow flowers of *M. verbenaceus* and *M. cardinalis* in 1988.

	Number of flowers			Bumblebee visits				Hummingbird visits			
Month:day:time	Red	Orange	Yellow	Red	Orange	Yellow	P	Red	Orange	Yellow	P
Mimulus verbenaceus											
8:08:1600	117	92	132	17↓[a]	29	62↑	<.001	23	40↑	3↓	<.001
8:09:0750	115	73	116	16↓	36	131↑	<.001	70	70↑	18↓	<.001
8:09:1705	115	73	116	2↓	21↓	124↑	<.001	171	167↑	135↓	<.001
8:10:0815	145	90	143	84↓	129↑	190↑	<.001	13	10	3	<.001
8:10:1640	145	90	143	13↓	56	202↑	<.001	40↓	80↑	38↓	<.001
8:11:0810	175	83	177	84↓	106↑	237↑	<.001	60	50↑	0↓	<.001
8:12:0805	200	111	198	96↓	97	160	<.001	196	166↑	99↓	<.001
8:12:1700	200	111	198	5↓	9↓	120↑	<.001	168	147↑	163	<.001
8:13:0855	180	83	175	54↓	66	172↑	<.001	115	63↑	56↓	<.001
8:13:1800	180	87	175	3↓	4↓	160↑	<.001	44	31↑	2↓	<.001
8:14:0815	212	81	165	27↓	37	162↑	<.001	71	64↑	24↓	<.001
8:15:0740	184	94	183	39↓	36	167↑	<.001	54	37	38	<.010
8:15:1700	184	94	183	2↓	3	50↑	<.001	7	2	2	<.300
8:16:0830	206	112	153	14↓	8↓	174↑	<.001	21	30↑	0↓	<.001
8:17:0630	214	86	177	3↓	2↓	128↑	<.001	66	72↑	26↓	<.001
Mimulus cardinalis											
8:08:1600	79	47	61	36↓	59	89↑	<.001	28	25	1↓	<.001
8:09:0750	69	45	32	21↓	37	34↑	<.001	61	36	0↓	<.001
8:09:1705	69	45	32	18	8	22↑	<.001	137	117↑	24↓	<.001
8:10:0815	61	39	23	49	59	26	<.010	4	6	0	<.100
8:10:1640	61	39	23	48	10↓	48↑	<.001	81	53	12↓	<.010
8:11:0810	61	55	12	27↓	62	49↑	<.001	34	20	0	<.020
8:12:0805	65	51	18	33	26	34↑	<.001	63	95↑	13	<.001
8:12:1700	65	51	18	18	8	10	<.050	130	88	21	<.100
8:13:0855	64	42	14	35	40	17	<.010	59	41	0↓	<.010
8:13:1800	89	81	14	28	15	16↑	<.001	91	92	14	<.300
8:14:0815	83	69	15	39	24	19↑	<.001	77	52	3↓	<.020
8:15:0740	53	71	15	20	33	26↑	<.001	55	58	0↓	<.001
8:15:1700	53	71	15	13	4	6↑	<.010	11	24	0	<.010
8:16:0830	79	78	21	18↓	21	34	<.001	34	74↑	0↓	<.001
8:17:0630	89	79	18	19↓	47	12	<.001	20↓	115↑	4↓	<.001

[a] ↑ or ↓ = significantly high or low, see text.

RESULTS

Pollinators showed clear, very highly significant ($p < .001$) preference for or avoidance of yellow flower color, but less clear preferences for or avoidance of orange or red flower colors. Bumblebees—principally *Bombus appositus* and *B. huntii*—strongly preferred yellow in both *M. verbenaceus* and *M. cardinalis*. Difference in shape did not appear to matter. Hummingbirds—principally *Selasphorus platycerus*—strongly eskewed yellow in both species (Tables 2, 3). Again, difference in shape did not appear to matter.

Hummingbirds significantly ($p < .001$) preferred orange *M. verbenaceus* flowers and showed a tendency to prefer orange *M. cardinalis* flowers as well (Tables 2, 3). This preference for orange over red flowers should not have been surprising in view of the fact that orange and red are equally conspicuous to hummingbirds (Grant and Grant 1968, Raven 1972).

Strong preferences and aversions for yellow are particularly interesting because yellow is the mutant color in both species. So, a new yellow mutant of either species would be preferentially visited by bumblebees and preferentially avoided by hummingbirds, but not in all-or-none reactions. Apparently then, with the species of pollinators tested, we are seeing the establishment of real, but partial, reproductive isolation due to the mutation of a single pair of color genes.

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SOIL LOOSENING PROCESSES FOLLOWING THE ABANDONMENT OF TWO ARID WESTERN NEVADA TOWNSITES

Paul A. Knapp[1]

ABSTRACT—Soil compaction was measured at four sites within two abandoned mining camps in the western Great Basin Desert, Nevada. Bulk density and macroporosity values were generated from soil samples collected in areas of different land use intensities in camps that had been abandoned for approximately 70 years. Results show that significant differences remain in bulk density values between abandoned roads and undisturbed areas in both towns, and that the areas around foundation peripheries are still significantly more compacted in one town. There were no significant differences between land use groups as measured by macroporosity. Estimated soil recovery, based on a linear model using bulk density values, suggests that approximately 100 to 130 years are necessary for complete loosening to occur for abandoned roads, and that 100 or fewer years are necessary for complete amelioration of the foundation periphery areas. The wetter townsite, with more freeze-thaw days, finer-grained soils, and greater plant cover, had shorter recovery estimates. These findings suggest that the results of human-use impacts in arid areas may still be apparent long after disturbances cease.

Key words: soil recovery, soil compaction, arid lands, Great Basin Desert, ghost towns.

Arid lands are undergoing environmental degradation processes at a rapid rate worldwide and are being severely disturbed by excessive soil erosion and salinization (Allen 1988, Goudie 1990). The explosion in human population levels in the last several decades in arid regions has been a major cause for land degradation, especially considering that arid regions are particularly sensitive to anthropogenic land use impacts (Goudie 1990). While the greatest extent of soil degradation has occurred in Sahelian Africa, other arid zones of the world are also vulnerable (Goudie 1990).

The arid American West is one such region where human use impacts have risen dramatically in the last several decades (Francis and Ganzel 1984). The increased popularity of backcountry visits by off-road vehicles, mountain bikes, backpackers, or horseback riders has had a considerable impact on the surrounding environment, either damaging or altering both the flora and soils of affected areas (Cole 1983, 1987, 1990, Lathrop 1983, Webb 1983, Prose and Metzger 1985).

Compaction of desert soils caused by backcountry activities can decrease infiltration rates, increase runoff, and impede plant root growth, which favors further soil degradation processes (Vollmer et al. 1976, Rowlands and Adams 1980, Hinckley et al. 1983, Lathrop 1983, Prose et al. 1987, Goudie 1990). While the impacts of backcountry activities have been documented over short time spans (often less than 30 years), little is known about long-term consequences of these activities (Knapp 1991). Few studies exist that document how well a disturbed area recovers following cessation of disturbances, particularly in areas traditionally considered to have little economic value, such as arid lands.

Recovery processes of compacted soils are not well understood (Webb et al. 1983, 1986) and have been conducted primarily in more mesic environments (Webb et al. 1983, Knapp 1989). Recovery estimates vary considerably, ranging from less than 10 years on Minnesota forest soils (Thorud and Frissell 1976), to 23 years on Idaho forest soils (Froehlich et al. 1985), to 50 years on forest soils in South Australia (Greacen and Sands 1980), and up to 200 years on soils in southwestern Montana (Knapp 1989).

The few studies that have examined soil recovery rates in the arid American West have been confined to the Mojave Desert (i.e., Webb and Wilshire 1980, Webb et al. 1983, 1986, 1988, Prose and Metzger 1985). Rates of soil recovery from these studies of abandoned mining camps ranged from 80 to 140 years and

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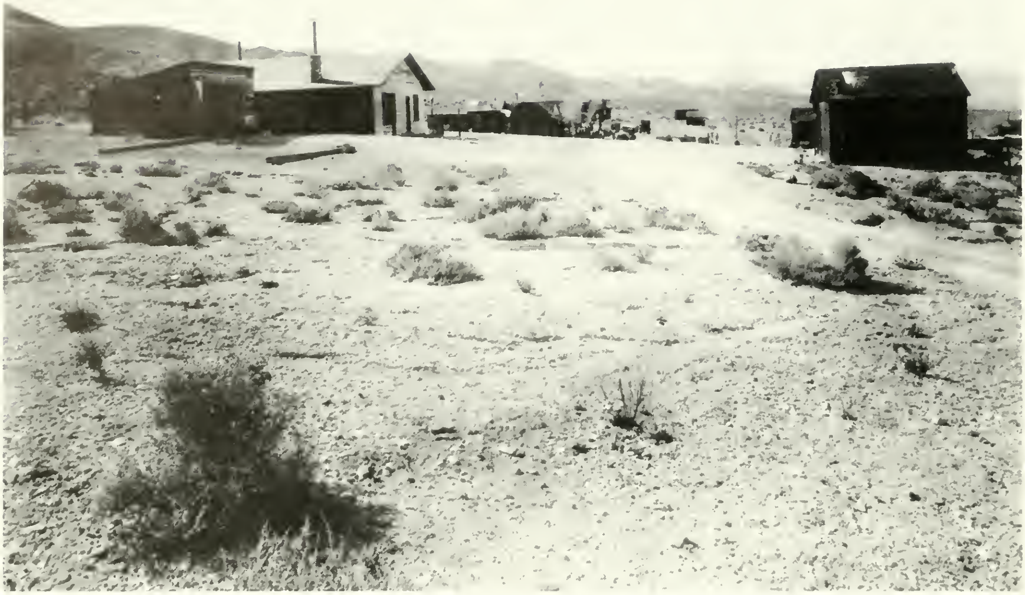

Fig. 1a. Terrill, ca 1920, looking northwest. Photo by Roly Ham, courtesy Special Collections, University of Nevada, Reno, Library.

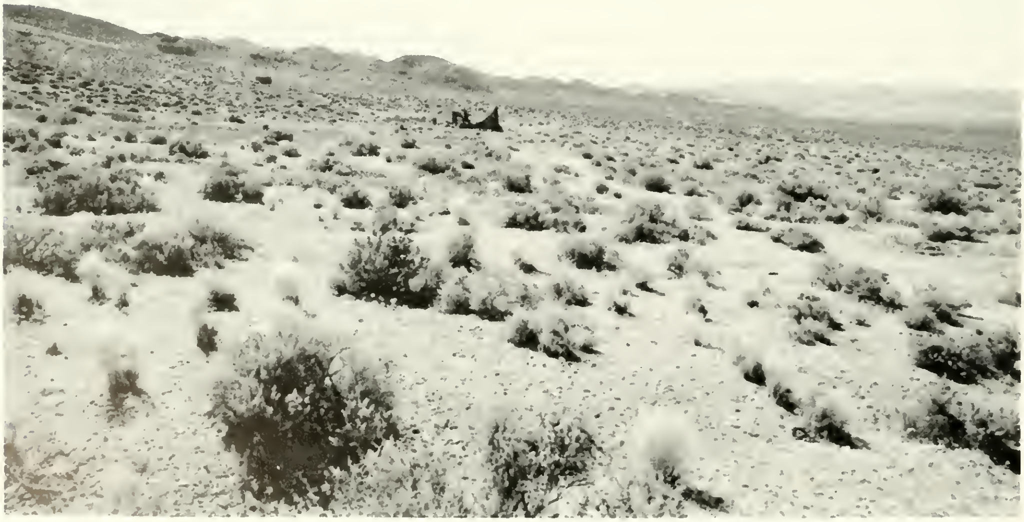

Fig. 1b. Terrill, 1990. Photograph by author.

averaged 100 years. Comparable studies have yet to be conducted in the Great Basin Desert.

Ghost towns abandoned in the early twentieth century in the western Great Basin Desert showcase the long-term effects of soil compaction. Built because of the discovery of valuable ores such as gold and silver, these towns were short-lived as the ores became too scarce to extract profitably (Paher 1970, Carlson 1974, Shamberger 1974). These towns have been

TABLE 1. Climatic and soils data for the two selected Great Basin Desert townsites.

Townsite	Elevation (m)	Est. annual precipitation (mm)	Est.* mean Jan. temp. (°C)	Est.* mean July temp. (°C)	Soil type	Sand, silt and clay (%)
Terrill	1305	125	−0.8	22.8	loamy sand	84/12/4
Wonder	1740	250	−3.9	20.5	sandy loam	46/50/4

*Source of estimate: Houghton et al. 1975.

exposed to a variety of environmental impacts, including trampling by livestock, humans, and vehicles, and have shown a variety of vegetation recovery responses (Knapp 1992). The purpose of this paper is to examine the effects of soil recovery in two abandoned mining towns in the Great Basin Desert in similar fashion to those studies conducted in the Mojave Desert.

STUDY AREAS

Two measures of soil compaction, bulk density and percentage macroporosity, were gathered from Terrill and Wonder. Terrill (39°05′N, 118°46′W) and Wonder (39°35′N, 118°04′W) were abandoned in ca 1915 and ca 1925, respectively (Figs. 1a, 1b). Both sites lie at the base of north-south trending fault-block mountain ranges in central western Nevada, although Terrill's elevation (1305 m) is substantially lower than Wonder's (1740 m). Terrill is the drier site, receiving approximately 130 mm of precipitation annually with the estimated mean January and July temperatures being −0.8 C and 22.8 C, respectively (Houghton et al. 1975; Table 1). The vegetation in Terrill is a salt desert scrub habitat type (Tueller 1989), and common species are the shrubs *Sarcobatus baileyi*, *Atriplex confertifolia*, and *Tetradymia spp.;* the grasses *Oryzopsis hymenoides* and *Bromus tectorum;* and the forb *Sphaeralcea ambigua*. Ground cover in Terrill is approximately 20% (Knapp 1992). Wonder receives approximately 250 mm of annual precipitation, has mean January and July temperatures of −3.9 C and 20.5 C, respectively (Houghton et al. 1975; Table 1), and supports a sagebrush/grass habitat type (Tueller 1989) with approximately 35% ground cover (Knapp 1992). Common species in Wonder are the shrub *Artemisia tridentata* and the grasses *B. tectorum* and *Sitanion hystrix*.

Both townsites have alluvially deposited, volcanic sandy-loam to loamy sand soils (Stewart and Carlson 1978; Table 1). The soils in Terrill are sandy, mixed, Typic Calciorthids, while Wonder's soils are fine-loamy, mixed, Typic Calciorthids (USDA-SCS 1975). Organic matter was estimated to be less than 1% at both townsites.

Terrill and Wonder have been subjected to minimal human-caused impacts since abandonment because of their remote locations. Little grazing by domestic animals has occurred in Terrill because of the lack of a nearby water source. Wonder has experienced greater grazing pressures by sheep, cattle, and feral horses. Neither sheep nor cattle have grazed the Wonder area since 1980 (A. Anderson, District Range Conservationist, BLM, personal communication, 1990).

METHODS

Soil samples for bulk density and macroporosity measurements were gathered at four different land use categories at each town. Data were collected from active roads (to get a theoretical upper limit of compaction), abandoned roads (representing prior high-intensity land use), areas within 5 m of foundation peripheries (representing prior moderate-intensity land use), and control plots (areas of minimal disturbance located near [<2 km] the townsite). All efforts were made to ensure that the four different land use groups within each townsite were similar to each other in terms of slope, aspect, soil texture, elevation, and parent material so that accurate comparisons could be made. Trails caused by either feral horses or small mammals were avoided.

Soil data from the controls, active roads, and abandoned roads were gathered using a stratified, unaligned sampling method. Thirty 5-m line transects were set parallel to both the active and abandoned roads, and one soil core was gathered at a random point along each line transect. Soil cores from control plots were gathered at a random point on each of forty 5-m line transects. Soil cores were also gathered at a

TABLE 2. Bulk density and macroporosity values, and recovery period estimates for abandoned townsites.

Site	Bulk Density[a] (g/cm^3)	Macroporosity (% by vol.)	Recovery period (years)	
			Bulk density	Macroporosity
		Terrill		
Active road	1.65 ± 0.04[b]	19.7 ± 2.4[b]		
Abandoned road	1.51[#°] ± 0.05	21.6[#] ± 2.3	130	120
Foundation peripheries	1.47[#] ± 0.07	21.9[#] ± 2.7	100	100
Control plot	1.41[#$] ± 0.03	22.7[#] ± 2.4		
		Wonder		
Active road	1.59 ± 0.08	17.3 ± 2.0		
Abandoned road	1.48[#°] ± 0.07	20.3[#] ± 1.9	100	80
Foundation peripheries	1.46[#] ± 0.07	20.8[#] ± 0.8	85	70
Control plot	1.42[#] ± 0.06	21.1[#] ± 1.1		

[a] Bulk density data with exception of active roads and standard deviation values are from Knapp 1992.
[b] One standard deviation.
[#] = Significantly different (p = .05) from active road based on Tukey test.
[°] = Significantly different (p = .05) from control plot based on Tukey test.
[$] = Significantly different (p = .05) from foundation peripheries based on Tukey test.

random point on each of forty 5-m line transects that were set perpendicular to the foundation periphery sides. The cores were oven-dried overnight and then weighed for bulk density (Blake 1965). One-fourth of the cores also were kept intact for macroporosity readings that were measured under 30 cm of tension using a tension-table (Orr 1960). Soil texture was measured using the micro-pipette method (Miller and Miller 1987).

Analysis of variance (ANOVA) was used to examine whether differences in either bulk density or macroporosity values existed between land use categories (abandoned roads, foundation peripheries, and control plots) for each town (Zar 1984, SAS 1985). Where significant overall differences existed, Tukey multiple comparison tests were used to determine between which groups these differences occurred (Zar 1984). Soil recovery was considered complete when no significant differences existed between disturbed sites and their respective control plots.

Soil recovery estimates were based on the equation (corrected from Webb et al. 1986):

$$T = [(I_a - I_u)/(I_a - I_t)] \circ T_A$$

where I_t = townsite (either abandoned road or foundation periphery)
I_u = undisturbed soils (control plots)
I_a = active road
T_A = time since abandonment of townsite

The data collected from active roads were used only for estimates generated by this equation. This equation generates rough estimates of soil recovery times. Webb et al. (1986) state that an exponential decay model might give more realistic soil recovery estimates, although only one abandonment time per site excludes the use of the exponential decay model.

RESULTS

Bulk density measurements for the abandoned road (1.51 g/cm^3) and foundation peripheries (1.47 g/cm^3) were significantly greater than for the control plot (1.41 g/cm^3) in Terrill, but in Wonder only the abandoned road (1.48 g/cm^3) had significantly greater bulk density values than the control plot (1.42 g/cm^3) (Table 2). Macroporosity measurements in both Terrill and Wonder were not significantly different between land use categories.

Estimated recovery times ranged from 85 to 130 years when based on bulk density measurements, and from 70 to 120 years when based on macroporosity measurements (Table 2). All measurements were greater on abandoned roads than on foundation peripheries and were comparatively longer in Terrill than in Wonder. While these values are derived by a linear recovery model, it is most likely that soil recovery follows more of a nonlinear path with rapid recovery early, then recovery rates slowing.

Heinonen (1977) has suggested that the bulk density of soils may decrease to a certain point, then level off without reaching predisturbance conditions.

DISCUSSION

Soil loosening is dependent upon shrink-swell, freeze-thaw, and biological activity processes (Larson and Allmaras 1971, Akram and Kemper 1979, Webb 1983, Webb et al. 1986, Knapp 1989). These processes in turn may be a function of soil type, climate, and biological activity. The recovery times for Terrill and Wonder show a relationship to all three of these processes, with recovery times in Terrill being longer than those in Wonder.

Soil texture is important because finer-grained soils are more prone to freeze-thaw and shrink-swell loosening processes than are coarser-grained soils (Webb et al. 1986). Fine-textured soils have more total pore space and have a higher water-holding capacity, thereby providing the soils of Wonder, that are more fine-grained than Terrill, more opportunities for expansion-contraction processes to occur (Millar et al. 1958). While percentages of clay may also be important, particularly if the clay has a high shrink-swell ratio, total amounts of clay at the two towns were the same and should not have a greater effect at one place than at the other.

Climate plays an important role in soil loosening processes, particularly where there is a high frequency of wetting and drying, freezing and thawing, or heating and cooling processes. Three climatic features favor faster soil loosening processes in Wonder than in Terrill. First, Wonder is 435 m higher than Terrill and Wonder has a shorter freeze-free period by approximately a month to a month and a half (J. James, Nevada State Climatologist, personal communication 1991). Second, Wonder lies at the base of a bowl-shaped depression and receives maximum cold-air drainage. Typical diurnal temperature contrasts for Wonder range from 22 to 28 C, with the greatest contrasts occurring in the summer and the least contrast in the winter (Houghton et al. 1975, J. James, personal communication, 1991). Terrill, on the other hand, experiences a 16.5 to 22 C diurnal temperature range (Houghton et al. 1975, J. James, personal communication, 1991). These differences in diurnal temperature range suggest that the heating-cooling and expansion-contraction processes are more pronounced for Wonder. Third, Wonder receives approximately twice as much annual precipitation as Terrill; therefore, the freezing-thawing and wetting-drying processes should occur more often in Wonder, facilitating the soil loosening processes.

Biological activity through plant root growth can also ameliorate soil compaction. Grasses and forbs are particularly effective for loosening of topsoil because they have many diffuse, shallow roots that penetrate the topsoil with subsequent minimal increases in soil strength, but leave behind small channels after the roots die (Webb et al. 1983). Plants such as shrubs, with a central taproot, however, cause localized compaction around the root, yet have fewer roots per unit volume and are less effective for soil loosening (Webb et al. 1983). Total plant cover in Wonder was substantially (approximately 20%) greater than in Terrill, especially with the grasses *Bromus tectorum* and *Sitanion hystrix*, which both have extensive, shallow root systems. Therefore, it appears that if soil loosening can be attributed to biological activity, it would be more pronounced in Wonder than in Terrill, although controlled, detailed experiments are necessary for confirmation.

CONCLUSIONS

After 75 years of recovery, significant differences remain between disturbed and undisturbed sites in Terrill as measured by bulk density. Estimates for recovery based on bulk density are from 100 to 130 years. In Wonder, after 65 years of recovery, significant differences remain only between abandoned roads and control plots. Estimated recovery for the abandoned road is 100 years. These results are in close agreement with similar, previous studies that examined soil recovery times in the Mojave Desert (e.g., Webb and Wilshire 1980, Webb et al. 1986) and suggest that the results of soil compaction processes that occur in arid environments are long-lived, but are not irreversible.

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BIOCHEMICAL DIFFERENTIATION IN THE IDAHO GROUND SQUIRREL, *SPERMOPHILUS BRUNNEUS* (RODENTIA: SCIURIDAE)

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ABSTRACT.—*Spermophilus brunneus* is restricted to a 90 × 125-km area of west central Idaho, with two distinct (northern and southern) groups of populations within this limited range. Morphological differences in pelage length and coloration, external and cranial measurements, and bacula suggest that these groups are either very distinct subspecies or species. We used starch-gel electrophoresis to estimate the amount of genetic differentiation accompanying these morphological differences by assaying genetic variation at 31 loci in the two geographic groups. Fifteen loci were polymorphic (13 in the northern group, 12 in the southern), and mean heterozygosity ($\bar{H}$) was high (12.3% northern and 10.8% southern). Nei's genetic distance (0.057) is in the range usually associated with subspecific differences. However, Jaccard's association coefficient (0.893) is about the same as that found between several ground squirrel taxa currently recognized as species. The high levels of heterozygosity suggest that *S. brunneus* is a neoendemic rather than a paleoendemic species.

Key words: Spermophilus brunneus, Spermophilus, *Idaho ground squirrel, ground squirrels, electrophoresis, taxonomy, biochemical differentiation.*

Spermophilus brunneus is one of the rarest, least studied, and most geographically restricted of the North American ground squirrels. Within its restricted range of ca 90 × 125 km in west central Idaho there are two well-differentiated subspecies, *S. b. brunneus* and *S. b. endemicus* (Yensen 1991). Significant differences in pelage length and color, external and cranial measurements, and bacular morphology suggest that the two taxa may be close to species-level separation (Yensen 1991). The northern *Spermophilus b. brunneus* is known from only ca 20 isolated sites in mountain meadows in Adams and Valley counties. These demes consist of <200 individuals and are separated from each other by distances of 1–70 km. In contrast, the southern *S. b. endemicus* is patchily distributed over a contiguous area 70 km long and up to 20 km wide in the lower-elevation foothills of Gem, Payette, and Washington counties (Yensen 1991).

Davis (1939) divided the North American species of subgenus *Spermophilus* into "small-eared" and "large-eared" groups and placed *S. brunneus* within the large-eared group. Nadler et al. (1973) found, however, that the karyotypes of *S. brunneus* and *S. townsendii mollis* (small-eared group) differed only in the presence or staining intensity of minor bands on six chromosomes, indicating a close affinity between *S. brunneus* and the small-eared group. Nadler et al. (1974) analyzed serum transferrins of *S. brunneus* using starch-gel electrophoresis and concluded that it was biochemically "intermediate" and possibly ancestral to both the Nearctic "small-eared" and "big-eared" species groups of subgenus *Spermophilus.* Nadler et al. (1982) extended their analysis to 21 Holarctic species using 18 loci and concluded that *S. brunneus* was a paleoendemic species most closely related to the Eurasian *S. dauricus.* Nadler et al. (1984) revised their phylogeny to incorporate chromosomal data and placed the evolutionarily conservative *S. brunneus* within the *S. townsendii* group.

The present study was conducted to estimate the genetic differentiation accompanying the substantial morphological differences between the two geographic groups of *S. brunneus* and to assess the hypothesis that *S. brunneus* is a paleoendemic species with small, relictual populations.

MATERIALS AND METHODS

Specimens Analyzed

A total of 82 specimens were analyzed from the following localities: *Spermophilus brunneus*

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brunneus—Adams Co.: 1 mi NE Bear Guard Station, 3; Bear Cemetery, 2; Cold Springs Cr., 1; Little Mud Cr., 5; Mill Cr. 3 mi N Hornet Guard Station, 2; New Meadows, 12; Price Valley, 2; Lick Cr., 6; Summit Cr., 9. *Spermophilus brunneus endemicus*—Gem Co.: Sucker Cr. 11 mi N Emmett, 20; 12.6 mi N Emmett, 1; Payette Co.: Big Willow Cr., 1; Dry Cr. Road, 3; Washington Co.: Lower Mann Cr., 10; Weiser Cove, 5. These specimens have been deposited as vouchers in the Albertson College Museum of Natural History.

Laboratory Methods

Blood was collected from the suborbital sinus of living animals (samples sizes were 21 *S. b. brunneus*, 9 *S. b. endemicus*). Liver and kidney tissues were from sacrificed animals (10 *S. b. brunneus*, 6 *S. b. endemicus*) or frozen carcasses collected for other purposes (18 *S. b. brunneus*, 31 *S. b. endemicus*). Carcasses were stored at −20 C for 1–6 months.

Tissue sample preparation and horizontal starch-gel electrophoresis follow Selander et al. (1971) with slight modifications. We used 11.0% electrostarch for lithium hydroxide gels and 12.4% for all other gels. Enzyme locus designations follow standardized Enzyme Commission (E.C.) nomenclature (Harris and Hopkinson 1976). The enzymes and nonenzymatic proteins screened in this study, with tissue and buffer systems used, were: alcohol dehydrogenase, E.C. No. 1.1.1.1 (ADH), liver, tris-citrate, pH 8.0; glycerol-3-phosphate dehydrogenase, E.C. No. 1.1.1.8 (GPD), liver, tris-citrate, pH 8.0; L-iditol dehydrogenase, E.C. No. 1.1.1.14 (IDDH), liver, tris-citrate, pH 8.0; lactate dehydrogenase, E.C. No. 1.1.1.27 (LDH), kidney, tris-citrate, pH 8.0; malate dehydrogenase, E.C. No. 1.1.1.37 (MDH), liver, tris-citrate, pH 6.3; isocitrate dehydrogenase, E.C. No. 1.1.1.42 (ICD), kidney, tris-citrate, pH 8.0; superoxide dismutase, E.C. No. 1.15.1.1 (SOD), kidney, tris-maleate or tris-citrate, pH 8.0; aspartate aminotransferase, E.C. No. 2.6.1.1 (AAT), liver, lithium hydroxide; hexokinase, E.C. No. 2.7.1.1 (HK), kidney, tris-citrate, pH 8.0; phosphoglucomutase, E.C. No. 2.7.5.1 (PGM), kidney, tris-citrate, pH 8.0; esterase, E.C. No. 3.1.1.1 (ES), hemolysate, tris-hydrochloric acid; peptidase, E.C. No. 3.4.11 or 13.° (PEP), liver, tris-citrate, pH 6.3; hemoglobin (HGB), hemolysate, tris-hydrochloric acid; albumin (ALB), plasma, lithium hydroxide; transferrin (TRF), plasma, lithium hydroxide; general proteins (GP1 and GP2), hemolysate, tris-hydrochloric acid; and general proteins (GP3 and GP4), plasma, tris-hydrochloric acid. The proteins were numbered in order of decreasing mobility, with the most anodal labeled 1.

The buffer and stain systems for the proteins screened in this study were described by Selander et al. (1971), except for stains for IDDH, HK, and PEP (Gill et al. 1987). Of the esterases, only acetylesterases were stained and were numbered 1 (most anodal) to 5. PEP-C was detected with L-leucyl-L-alanine. ADH does not have to be stained specifically and is seen on many dehydrogenase gels. It was read on gels stained for GPD.

Computational Methods

Gene frequencies, measures of genetic variation, Nei's (1978) unbiased genetic distance and unbiased genetic identity, and the average inbreeding coefficient (F_{ST}) were derived from input on single individual genotypes (electromorphs) using the computer program BIOSYS-1 (Swofford and Selander 1981). Jaccard's association coefficient, $S_J = a/(a+u)$, where a = the number of matched electromorphs (1:1) and u = the number mismatched (1:0 or 0:1) (Sneath and Sokal 1973), was also calculated for the two groups. S_J depends only upon the presence (1) or absence (0) of alleles, as indicated by bands on the starch gels (electromorphs), not on allelic frequencies as do measures of genetic distance. Negative matches were excluded.

Results and Discussion

Spermophilus b. brunneus was polymorphic at 13 loci (42%), whereas *S. b. endemicus* was polymorphic at 12 loci (39%). If esterases are excluded, polymorphism is reduced to 31%, which is similar to the 29% reported for *Mus musculus* and *Homo sapiens* (Lewontin 1974). Average number of alleles per locus ($\bar{A}$) was 1.48 ± 0.11 ($\bar{X}$ ± SE) in *S. b. brunneus* and 1.48 ± 0.12 in *S. b. endemicus*. All polymorphic loci had two alleles, except for peptidase and two of the esterases, which had three.

Mean heterozygosity per individual per locus in our sample was 12.3 ± 3.7% in *S. b. brunneus* and 10.8 ± 3.9% in *S. b. endemicus*. These values are much higher than the 2.7% heterozygosity reported by Nadler et al. (1982)

for *S. b. brunneus.* The loci common to both studies, however, were less variable than some of our 18 additional loci. Even if esterases are excluded from the analysis, our measures of genetic variability (*S. b. brunneus,* $\bar{H} = 8.2\%$, $\bar{A} = 1.35$; *S. b. endemicus,* $\bar{H} = 7.4\%$, $\bar{A} = 1.38$) are still much higher than theirs. They found H values of 0.0–10.4% ($\bar{X} = 3.5\%$) for other species of *Spermophilus.* Cothran et al. (1977) found high heterozygosity (9.3%) in the ground squirrel subgenus *Ictidomys.* The average heterozygosity for 26 taxa of rodents was 5.4% (Selander 1975), so Idaho ground squirrels have relatively high levels of heterozygosity. Thus, the levels of genetic variability are high for a species postulated to be a paleoendemic (Nadler et al. 1974, Cothran et al. 1977, Nadler et al. 1982) with small isolated demes and confined to a small geographic area (Yensen 1991).

Sixteen of 31 protein systems scored for *S. brunneus* were monomorphic (GPD, LDH-A, ICD-2, HK-1,2, PGM-1,2, AAT-1,2, IDDH, SOD-B, ADH, ALB, TRF, GP-1,2). Frequencies of alleles in the polymorphic systems (the most common allele <0.99) are shown in Table 1. As in other species (Kojima et al. 1970, Lewontin 1974), non-glucose–metabolizing enzymes were more polymorphic than glucose-metabolizing enzymes with five monomorphic (AAT-1,2, IDDH, SOD-B, and ADH), while PEP-C, SOD-A and all five esterases were polymorphic (Table 1). The two taxa of *S. brunneus* did not differ substantially in glucose-metabolizing enzymes, with the majority of loci monomorphic, and the same allele common in the polymorphic loci.

Nadler et al. (1982) found LDH to be monomorphic in all 21 North American and Eurasian *Spermophilus* species examined. However, we found two individuals of *S. b. brunneus* that were homozygous for a fast allele at the LDH-B locus. Nadler et al. (1982) assayed from LDH in red blood cells while we used kidney extracts, so the difference may be between the two tissues. Both groups of *S. brunneus* were polymorphic for ICD-1 and HK-3, while only *S. b. endemicus* was polymorphic for MDH-1.

Of the enzymes not involved in glucose metabolism, the esterases were the most variable (Table 1). We also found considerable differences between *S. b. brunneus* and *S. b. endemicus* in the other non-glucose–metabolizing enzymes. Different alleles were common for PEP-C and ES-4 in the two groups of *S. brunneus.* In both cases the differences were in allelic frequency rather than in the presence or absence of alleles.

TABLE 1. Allelic frequencies of polymorphic loci in *Spermophilus brunneus.*

Locus°	Allele°°	*brunneus*	*endemicus*
GLUCOSE-METABOLIZING ENZYMES			
LDH-B	a	0.929	1.000
	b	0.071	0.000
MDH-1	a	0.000	0.018
	b	1.000	0.911
	c	0.000	0.071
ICD-1	a	0.926	0.986
	b	0.074	0.014
HK-3	a	0.132	0.097
	b	0.868	0.903
NON-GLUCOSE-METABOLIZING ENZYMES:			
SOD-A	a	0.786	0.957
	b	0.214	0.043
PEP-C	a	0.365	0.329
	b	0.135	0.343
	c	0.500	0.329
ES-1	a	0.179	0.056
	b	0.107	0.167
	c	0.714	0.778
ES-2	a	0.969	1.000
	b	0.031	0.000
ES-3	a	0.971	0.944
	b	0.000	0.056
	c	0.029	0.000
ES-4	a	0.714	0.389
	b	0.286	0.611
ES-5	a	0.656	0.944
	b	0.344	0.056
NONENZYMATIC PROTEINS.			
HGB-1	a	0.233	0.667
	b	0.767	0.333
HGB-2	a	0.100	0.500
	b	0.900	0.500
GP-3	a	0.000	1.000
	b	1.000	0.000
GP-4	a	0.962	0.750
	b	0.038	0.250

°See text for acronyms of loci.

°°Alleles are listed in order of increasing mobility; a is slowest

Nonenzymatic proteins were scored in both hemolysate and plasma. Albumin and transferrin in plasma and two general proteins in hemolysate were monomorphic. We found variability at the two hemoglobin loci and at two general protein loci in plasma (Table 1). Heterozygosity of hemoglobins has been found in the closely related Townsend's ground squirrel (*S. townsendii*), in which the two hemoglobins have identical α-chains and differ by only one amino acid in the sequence of their β-chains

(Kleinschmidt et al. 1985). They found no difference in the oxygen affinity of the two hemoglobins.

A general protein in plasma (GP-3) represented by a band just anodal to albumin distinguished the two *S. brunneus*. A fast allele apparently has reached fixation in *S. b. brunneus,* whereas a slow allele appears fixed in *S. b. endemicus* (Table 1). This is the only locus that can serve as a marker gene among the 31 loci scored, although LDH-B and MDH-1 had alleles that were fixed in one taxon and polymorphic in the other. The other presumed loci differed in allelic frequency only.

Nei's (1978) genetic distance is a measure of the accumulated number of gene differences per locus between populations. The genetic distance of 0.057 found between the two *S. brunneus* was within the range associated with subspecific differentiation (Avise 1974). The average inbreeding coefficient (F_{ST} = 0.167) indicated moderately high genetic differentiation. The two *S. brunneus* have a genetic identity of 0.944. By comparison, Cothran et al. (1977) found genetic identities of 0.808 between *S. spilosoma* and *S. mexicanus,* 0.835 between *S. spilosoma* and *S. tridecemlineatus,* and 0.965 between *S. tridecemlineatus* and *S. mexicanus* in the subgenus *Ictidomys.*

To compare our results with other results from the subgenus *Spermophilus* (Nadler et al. 1982), we also calculated Jaccard's association coefficient. This measure is less sensitive to sample size and depends on presence or absence of an allele, rather than on allelic frequencies. Jaccard's coefficient of similarity between the two groups of *S. brunneus* was 0.893. Judging from Figure 2 in Nadler et al. (1982:206), the similarity between the two groups of *S. brunneus* is about the same as the similarity between *S. armatus* and *S. beldingi,* or between some of the putative semispecies in the *S. townsendii* complex, the Eurasian *S. suslicus* and *S. citellus,* or *S. major* and *S. erythrogenys. Spermophilus richardsoni* and *S. elegans* are more similar electrophoretically than the two Idaho ground squirrels. However, direct comparisons are difficult since the similarity coefficients computed by Nadler et al. (1982) were based on a different, and apparently less variable, set of loci.

The electrophoretic data confirm that the two Idaho ground squirrels are genetically as well as morphologically differentiated taxa. The evidence does not clearly resolve the question of whether the two are separated at the subspecies or species level. The presence of one marker gene and the observed frequency differences at others could be consistent with either interpretation. The high levels of heterozygosity, however, do not support the paleoendemic hypothesis.

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NEW GENUS, *APLANUSIELLA*, AND TWO NEW SPECIES OF LEAFHOPPERS FROM SOUTHWESTERN UNITED STATES (HOMOPTERA: CICADELLIDAE: DELTOCEPHALINAE)

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ABSTRACT.—A new genus, *Aplanusiella* (type-species, *Aplanusiella utahensis*, n. sp.) and two new species, *A. utahensis* and *A. californiensis*, are described and illustrated. The two species are allopatric and coexist on the same host genus, (*Atriplex*) with members of a closely allied leafhopper genus, *Aplanus*. Notes on distribution of hosts and leafhoppers as well as leafhopper intergeneric relationships are also given.

Key words: leafhoppers, new species, new genus, Cicadellidae, Aplanusiella, *distribution, hosts.*

In a 1986–89 survey of rangeland leafhoppers of Utah (Haws et al. 1989), two populations were taken from *Atriplex* spp. and tentatively identified as members of the genus *Aplanus*. One population was later identified as *Aplanus albidus* (Ball) from shadscale, *Atriplex confertifolia* (Torr. & Frem.) Wats. The other population was collected from four-winged saltbush, *Atriplex canescens* (Pursh) Nutt. and is described herein as a new genus and new species closely allied to *Aplanus*. An additional new species is also described from specimens collected in California on *Atriplex* sp. Notes are given on the phytogeography of the host genus, *Atriplex*, the distribution of the two genera, and their taxonomic and host relationships.

The general habitus (form and color pattern) of the component populations are so remarkably similar that it is likely that additional material of the new taxa will be found in other repositories. Only after dissection and examination of the male genital structures will their true identity be revealed. Moreover, it is probable that additional new species will come to light after more thorough collecting is done on *Atriplex* spp. in southwestern United States and northern Mexico. This assumption is based on two additional populations of female specimens in hand from Nevada and California for which males are presently unknown and are required for definitive generic placement. The female seventh sternal characters appear to place these populations in the new genus (sensu stricto). Populations of these groups are rather rare in *Atriplex* host areas of the high- to low-desert regions of western North America.

Aplanusiella, new genus

TYPE SPECIES.— *Aplanusiella utahensis*, n. sp.

Small, rather slender species. Related to *Aplanus* Oman but smaller and with distinctive male genital characters. General color light yellow to ivory with numerous, nearly concentric, tiny rufous spots on forewings, spots not usually forming lines as typically present in *Aplanus*, large spots in clavus and in apical crossveins of costa formed by aggregation of smaller spots, pronotum and scutellum sometimes with tiny spots.

Head narrower than pronotum, anterior margin obtusely angled and rounded to front, crown produced medially to about one and one-half times length next to inner margin of eye, disk somewhat depressed in middle but lacks transverse depression before apex as in *Aplanus*; pronotum and scutellum as in *Aplanus*; forewings with inner anteapical cell open basally, appendix well developed; clypeus and clypellus as in *Aplanus*.

Male pygofer with macrosetae in apical half and with prominent caudoventral spine, sometimes crossing over in caudal view; aedeagus small, base large in lateral view, apical half narrow, tubular, sometimes with small angulate protrusion at base of shaft on dorsal margin, gonopore subapical on ventral margin; connective short, Y-shaped, articulated with aedeagus; style broad, apophysis short; plate triangulate with row of macrosetae submarginally and row of microsetae marginally, female seventh sternum with short projection medially on caudal margin.

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Two allopatric species are known that occur in the southwestern states of Utah and California on desert shrubs of the genus *Atriplex*. *Aplanusiella* can be distinguished from *Aplanus* by the smaller size, by the absence of a preapical depression on the crown, by the presence of a prominent caudoventral pygofer spine, by the smaller aedeagus that lacks apical processes, and by the female seventh sternum that has a more distinctive spatulate process on the middle of the caudal margin.

Aplanusiella utahensis, n. sp.

Figs. 1a-1l

LENGTH.—Male 3.5–3.75 mm, female 4.00–4.20 mm.

General color pale yellow to ivory with numerous, nearly concentric, tiny rufous spots on forewings, large aggregate spots on apex of clavus and in apical crossveins of costa, sometimes with few similar spots on pronotum and scutellum. Related to *Aplanusiella californiensis*, n. sp., but with distinctive male genital and female seventh sternal characters.

MALE.—Pygofer in lateral view with long, stout caudoventral process that sometimes crosses its counterpart in caudal view, but usually closely appressed to caudal margin of pygofer (Fig. 1b); plate long, triangulate with uniserate macrosetae submarginally and uniserate microsetae marginally on outer margin (Fig. 1c); style in dorsal view long, broad in basal 2/3, apophysis short, curved and pointed apically (Fig. 1d); connective short, Y-shaped (Fig. 1e); aedeagus in lateral view short, ventral margin abruptly angled near middle, broad basally, shaft narrow, tubular with basal triangulate projection on either side of dorsal margin, gonopore subapical on ventral margin (Figs. 1f–1k).

FEMALE.—Seventh sternum broadly excavated on caudal margin, with prominent median spatulate process (Fig. 1l).

HOLOTYPE (male).—UTAH: Daggett Co., Brown's park, Pyke plots, roadside, 12.VI.1987, four-winged saltbush, *Atriplex canescens*, B. A. Haws (CAS). Paratypes, 1 male, Daggett Co., Brown's park, 3.5 mi E Jarvis ranch, 26.VI.1987, on four-winged saltbush, *Atriplex canescens*, Haws, Nelson (author's collection); 2 males, 1 female, San Juan Co., Dry Valley, 8.IX.1987, four-winged saltbush, *Atriplex canescens*, B. Haws, A. Issa (USU); 2 males, 2 females, Uintah Co., Bonanza, 14.VII.1975–3.IX.1976, *Atriplex canescens*, G. E. Bohart (USU); 1 male, Grand Co., Jughandle Potash Rd., 19.VIII.1987, four-winged saltbush, *Atriplex canescens*, B. A. Haws, C. R. Nelson (BYU); 1 male, Grand Co., Colorado River, Hwy 128, 6 mi NE jct. Hwy 191, 26.V.1987, *Atriplex canescens*, B. A. Haws, C. R. Nelson (USU).

REMARKS.—This species can be distinguished from *californiensis*, n. sp., by the longer caudoventral pygofer process, by the abruptly angled ventral margin of the aedeagus, by the presence of a small basal triangulate process on the dorsal margin of the aedeagal shaft, and by the prominent spatulate process on the middle of the female seventh sternum.

The species is known from the eastern counties of Utah bordering Colorado and is likely present in the western part of that state and in northern Arizona where the host occurs. Collection dates suggest that the species has two generations per year and presumably overwinters as eggs on its host.

Aplanusiella californiensis, n. sp.

Figs. 1m–1s

LENGTH.—Male 3.30–3.50 mm, female 3.60–3.80 mm.

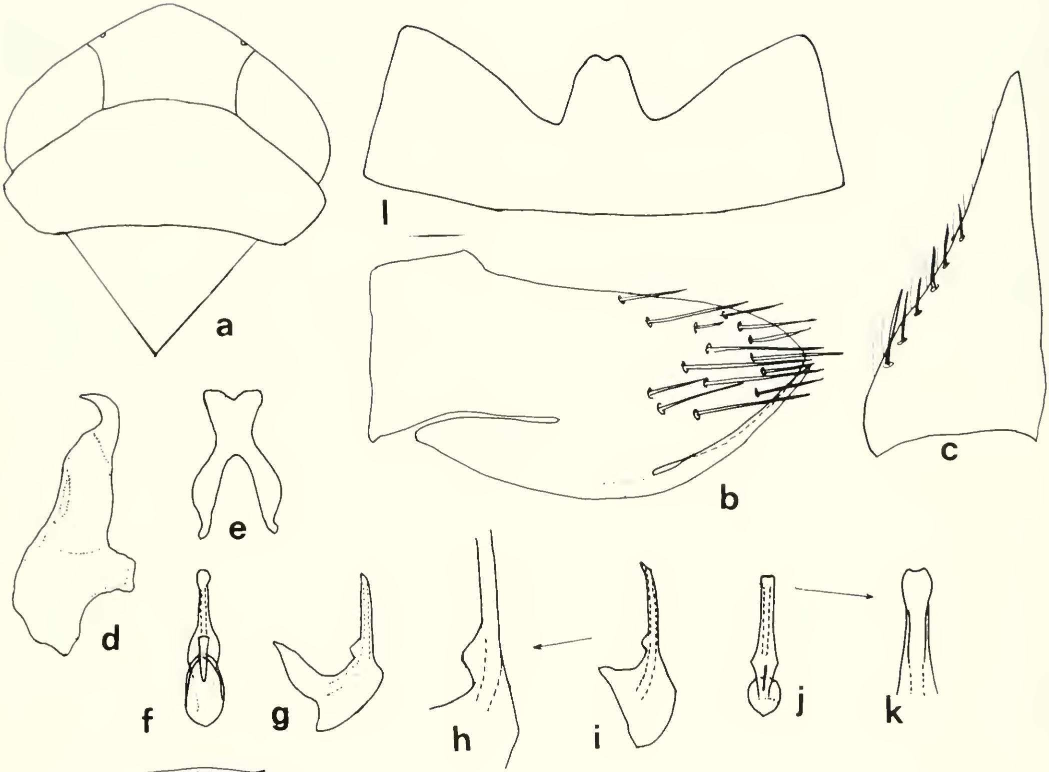
General color as in *A. utahensis*, n. sp., and related to that species but with distinctive male genital and female seventh sternal characters.

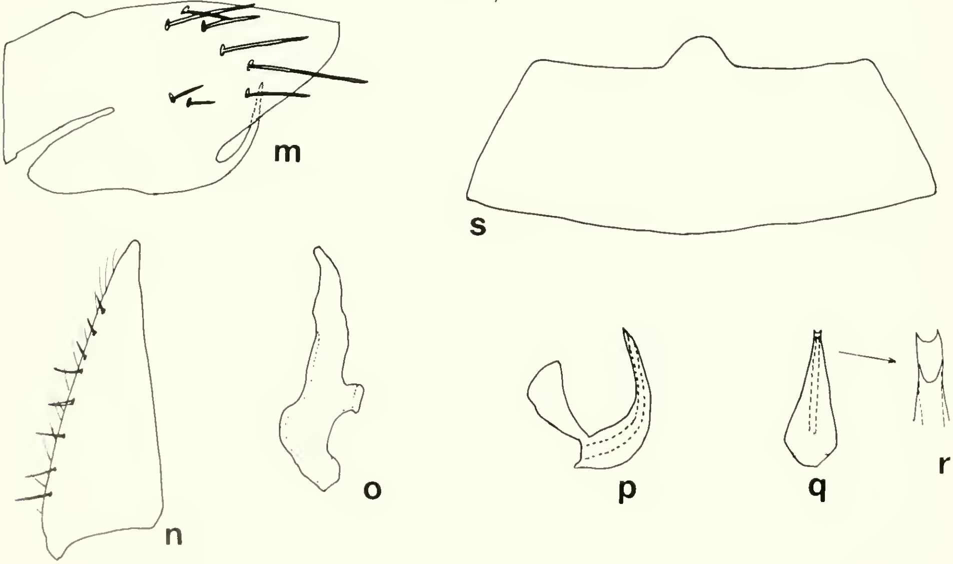
Head similar to *utahensis* except not as pointed apically.

MALE.—Pygofer in lateral view with moderately long caudoventral process that usually crosses its counterpart in caudal view, not closely appressed to margin of pygofer (Fig. 1m); plate long, triangulate, with row of marginal microsetae and submarginal macrosetae (Fig. 1n); style in dorsal view long, narrow, apophysis short, obliquely truncate apically (Fig. 1o); aedeagus in lateral view short, ventral margin gradually curved, apical third tubular, broad basally in ventral view, tapered toward apex, gonopore subapical on ventral margin (Figs. 1p–1r).

FEMALE.—Seventh sternum with truncate caudal margin except for short, median process (Fig. 1s).

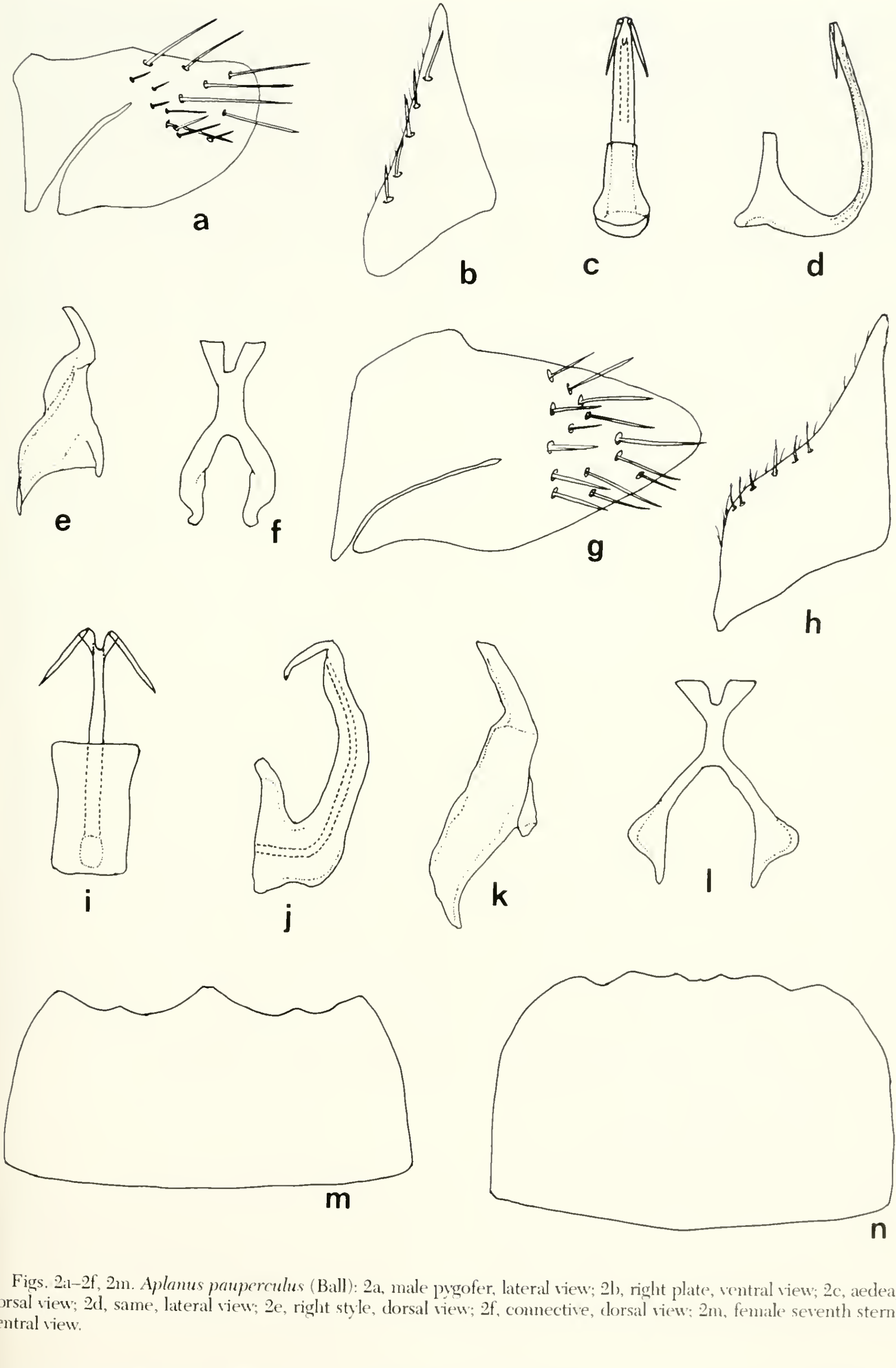
HOLOTYPE (male).—CALIFORNIA: Riverside Co., Indio, 12.I.1988, *Atriplex* sp., G. N.





Figs. 1a–1l. *Aplanusiella utahensis*, n. sp.: 1a, head, pronotum, and scutellum, dorsal view; 1b, male pygofer, lateral view; 1c, right plate, ventral view; 1d, right style, dorsal view; 1e, connective, dorsal view; 1f, aedeagus, dorsal view; 1g, same, lateral view; 1h, same (enlarged), showing triangulate process, lateral view; 1i, same (showing variation), lateral view; 1k, same (enlarged), showing apex of aedeagus, ventral view; 1l, female seventh sternum, ventral view.

Figs. 1m–1s. *Aplanusiella californiensis*, n. sp.: 1m, male pygofer, lateral view; 1n, right plate, ventral view; 1o, right style, dorsal view; 1p, aedeagus, lateral view; 1q, same, ventral view; 1r, same (enlarged), showing apex of aedeagus, ventral view; 1s, female seventh sternum, ventral view.



Figs. 2a–2f, 2m. *Aplanus pauperculus* (Ball): 2a, male pygofer, lateral view; 2b, right plate, ventral view; 2c, aedeagus, dorsal view; 2d, same, lateral view; 2e, right style, dorsal view; 2f, connective, dorsal view; 2m, female seventh sternum, ventral view.

Figs. 2g–2l, 2n. *Aplanus albidus* (Ball): 2g, male pygofer, lateral view; 2h, right plate, ventral view; 2i, aedeagus, dorsal view; 2j, same, lateral view; 2k, right style, dorsal view; 2l, connective, dorsal view; 2n, female seventh sternum, ventral view.

Oldfield (CAS). Paratypes, 2 males, 6 females, same data as holotype (OSU); 5 males, 16 females, Imperial Co., Brawley, 23.VIII.1983, *Atriplex* sp., J. Williams (OSU, BYU).

REMARKS.—This species can be separated from *utahensis* by the shorter caudoventral pygofer spine, by the smoothly curved ventral margin of the aedeagus, by the lack of a basal process on the aedeagal shaft, by the broader base of the aedeagus in ventral view, and by the truncate caudal margin and shorter median process of the female seventh sternum.

This species is known from southern California on *Atriplex* (species unknown) at elevations below sea level. Collection dates suggest that the species overwinters in the adult stage and may have as many as three generations per year.

Aplanus Oman

Aplanus Oman, 1949:138. Type species, *Eutettix pauperculus* Ball.

Only two species are known in the genus, both assigned by Oman (1949). Crowder (1952) treated the group with a key to species, redescriptions, and illustrations of the genital characters. The range of *Aplanus* is much broader in western United States than the presently known range of *Aplanusiella*.

Characters are given for *Aplanus pauperculus* (Figs. 2a–2f, 2m) and *Aplanus albidus* (Ball) (Figs. 2g–2l, 2n) to show generic relationships between them and species of *Aplanusiella*. In *Aplanus* the pygofer lacks the caudal spine, and the aedeagus is about twice as long with distinctive terminal processes. The female seventh sternum lacks the obvious median caudal process that is present in *Aplanusiella*. Ball (1900) reported that shadscale, *Atriplex confertifolia* (Torr. & Frem.) Wats., was the host of *Aplanus albidus*. The specific host of *A. pauperculus* is yet unknown.

Phytogeography of *Atriplex*

Four-winged saltbush (*Atriplex canescens*) is endemic to western North America. Its range extends from southern Canada to northern Mexico. Shadscale (*Atriplex confertifolia*) is also endemic, but its range is more restrictive within western United States (Stutz and Sanderson 1979, 1983, Sanderson et al. 1990). Both species produce hybrids between themselves and other species of *Atriplex*. However, autoploidy is the most common genetic mechanism in both species, which have produced a number of races throughout their range. These races and other ecotypes have been identified and mapped by these workers.

The biogeographical relationships between *Aplanus* and *Aplanusiella* species and their host species are poorly known. Although hosts have been identified for two leafhoppers (*Aplanus albidus* and *Aplanusiella utahensis*) of the four known species, nothing is known about the others nor has preference, if any, of these leafhoppers for races or ecotypes been studied in *Atriplex*. The role of *Atriplex* in the evolutionary development and speciation of the group is likewise unknown.

DEPOSITION OF TYPE SPECIMENS

The holotype specimens of *Aplanusiella utahensis* and *Aplanusiella californiensis* are deposited in the California Academy of Sciences, San Francisco (CAS); paratypes are in Oregon State University, Corvallis (OSU), Utah State University, Logan (USU), and Monte L. Bean Museum, Brigham Young University, Provo, Utah (BYU).

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SUMMER HABITAT USE BY COLUMBIAN SHARP-TAILED GROUSE IN WESTERN IDAHO

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ABSTRACT.—We studied summer habitat use by Columbian Sharp-tailed Grouse (*Tympanuchus phasianellus columbianus*) in western Idaho during 1983–85. Vegetative and topographic measurements were recorded at 716 locations of 15 radio-tagged grouse and at 180 random sites within the major vegetation/cover types in the study area. The mean size of summer home ranges was 1.87 ± 1.14 km^2. Of eight cover types identified in the study area, individual grouse used the big sagebrush (*Artemisia tridentata*) cover type more than or in proportion to availability, the low sagebrush (*A. arbuscula*) type in proportion to availability, and avoided the shrubby eriogonum (*Eriogonum* spp.) type. Characteristics of the big sagebrush cover type that Sharp-tailed Grouse preferred include moderate vegetative cover, high plant species diversity, and high structural diversity. Grouse used areas of dense cover (i.e., mountain shrub and riparian cover types) primarily for escape cover. Compared with random sites, grouse selected areas with (1) greater horizontal and vertical cover, (2) greater canopy coverage of forbs typically decreased by livestock grazing, (3) greater density and canopy coverage of arrowleaf balsamroot (*Balsamorhiza sagittata*), and (4) greater canopy coverage of bluebunch wheatgrass (*Agropyron spicatum*) in the big sagebrush cover type in 1984 and the low sagebrush cover type in 1985. The importance of the native perennials arrowleaf balsamroot and bluebunch wheatgrass became apparent during a drought year when many exotic annuals dried up and provided no cover. Overall, grouse selected vegetative communities that were least modified by livestock grazing.

Key words: Tympanuchus phasianellus columbianus, *Columbian Sharp-tailed Grouse, Idaho, summer habitat characteristics, management.*

Columbian Sharp-tailed Grouse (*Tympanuchus phasianellus columbianus*) have declined in both numbers and distribution since European settlement, currently occupying <10% of their former range (Miller and Graul 1980). Degradation of native habitat by livestock grazing and agriculture are thought to be major factors in this decline (Yocom 1952, Aldrich 1963, Zeigler 1979). Overgrazing reduced bunchgrasses and perennial forbs that are important components of nesting and brood-rearing habitat (Yocom 1952, Jewett et al. 1953, Klott and Lindzey 1990). Conversion of range to cropland destroyed nesting and brood-rearing habitat and deciduous shrubs that are critical for winter food and escape cover (Zeigler 1979, Giesen 1987, Marks and Marks 1988). As a result, Columbian Sharp-tailed Grouse were designated as a candidate species for listing as federally threatened/endangered (Federal Register 1989).

Quantitative information on home range size and habitat preferences of Columbian Sharp-tailed Grouse throughout their range is lacking, especially data based on radio-tagged individuals during the summer reproductive period (see Klott and Lindzey 1990). We studied Columbian sharptails in areas with eight vegetation/cover types. The primary objective of our study was to provide information on summer habitat preferences by Columbian Sharp-tailed Grouse.

STUDY AREA

The 2000-ha study area is 23 km north of Weiser in Washington County, Idaho. Elevation ranges from 970 to 1188 m. Annual precipitation averages 39 cm. The springs and summers of 1983 and 1984 were relatively cool and wet, whereas those of 1985 were unusually hot and dry. Sharp-tailed Grouse had not been hunted in the study area since 1974.

Vegetation is characteristic of a shrubsteppe community (Marks and Marks 1987a). The greatest proportion of the study area (40%) was occupied by the big sagebrush (*Artemesia tridentata*) cover type; low sagebrush (*A. arbuscula*) and shrubby eriogonum (*Eriogonum*

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sphaerocephalum and *E. thymoides*) types occupied 21 and 20%, respectively. The remaining 19% of the study area was occupied by five other cover types (see below).

The big sagebrush cover type was dominated by big sagebrush, with lesser amounts of bitterbrush (*Purshia tridentata*) and low sagebrush. The greatest canopy coverage of bluebunch wheatgrass (*Agropyron spicatum*) was found in this cover type; arrowleaf balsamroot (*Balsamorhiza sagittata*) was the dominant forb. Bulbous bluegrass was the most common herbaceous plant in the understory of the low sagebrush cover type with lesser amounts of willoweed (*Epilobium paniculatum*), bluebunch wheatgrass, and Sandberg's bluegrass (*Poa sandbergii*). The herbaceous layer of the shrubby eriogonum cover type was relatively sparse and dominated by Sandberg's bluegrass. The mountain shrub cover type occurred in dense patches on hillsides; common species were bittercherry (*Prunus emarginatus*), common chokecherry (*P. virginiana*), snowbrush ceanothus (*Ceanothus velutinus*), and Saskatoon serviceberry (*Amelanchier alnifolia*). The shrub layer of the bitterbrush (*Purshia tridentata*) cover type was almost exclusively bitterbrush, while the herbaceous layer was similar to that found in the big sagebrush type. Riparian vegetation was dominated by Douglas hawthorn (*Crataegus douglasii*), with lesser amounts of willow (*Salix* spp.) and Woods rose (*Rosa woodsii*). Bulbous bluegrass (*Poa bulbosa*), an exotic grass, was widespread throughout the study area. Plant nomenclature follows Hitchcock and Cronquist (1976).

Two vegetation types were almost exclusively comprised of nonnative vegetation. A small portion of the study area contained agriculture, composed of dryland wheat and barley, and monocultures of intermediate wheatgrass (*Agropyron intermedium*) seedings.

The study area was grazed by livestock since at least 1900. Before about 1940, large bands of sheep were driven through the area. Since then, the major land use in the study area has been cattle grazing. No livestock grazing occurred during this study.

METHODS

Trapping and Monitoring

Grouse were captured on dancing grounds using funnel traps, mist nets, and drop nets. Sex was determined by examination of crown feathers (Henderson et al. 1967) and age by examination of outer primaries (Ammann 1944). Thirty-eight grouse (28 males and 10 females) of 46 captured were fitted with solar-powered radio transmitters attached to Herculite ponchos (Marks and Marks 1987b). Radios weighed between 13.5 and 14.5 g. Fifteen (13 males and 2 females) grouse provided data for home range and microhabitat analyses. The other 23 grouse with radios were relocated for two months or less as a result of mortality (Marks and Marks 1987b) or dispersal from the study area. Data from these birds were used in the microhabitat analyses but not in the calculation of home range size. Sample sizes were not large enough to compare habitat use or home range size between male and female grouse.

Radio-tagged grouse were monitored from May to September 1983–85. Each time a grouse was located, it was flushed (hereafter these locations are called flush sites). Flush sites served as focal points for habitat sampling and for calculation of home ranges. Grouse were located throughout the day and locations were stratified into four time intervals: sunrise to 0800, 0801 to 1100, 1101 to 1700, and 1701 to sunset. On average, each radio-tagged bird was flushed four days a week, once in each of the four time intervals.

Habitat Sampling

The study area boundary was determined by grouse movements during 1983. Cover types were digitized and areas calculated for each type using GEOSCAN (Software Designs 1984), a geographic information program. Flush sites were plotted and home range sizes (Mohr 1947) were calculated using the computer program TELDAY (Lonner and Burkhalter 1986).

Use vs. availability of cover types (i.e., macrohabitat) was assessed by (1) using the proportion of cover types within each bird's home range, and (2) using the proportion of cover types within a 1.2-km radius of the dancing ground at which each bird was captured. The 1.2-km radius around each of three dancing grounds (upper, middle, and lower) encompassed 90% of all grouse locations. Flush sites within 50 m of a dancing ground during the spring and autumn display periods were omitted from macrohabitat analyses.

We measured vegetation at each flush site (i.e., microhabitat) to estimate plant species composition, frequency, percent canopy coverage, and bare ground using a 20 × 50-cm frame (Daubenmire 1959). Five frames were read at each flush site: one at the approximate center and one in each of the four compass directions at randomly chosen distances of 2, 4, 6, or 8 m from the center location. Vertical structure of the vegetation was evaluated by a cover board that was a 16.5 × 49.5-cm rectangle. The cover board was placed at the center of the flush site and read twice from 5 m away in each of the four compass directions while the observer was prone and standing, respectively. A total reading of 150 squares was possible from each compass direction. In total, five canopy coverage and four cover board measures were taken at each site. Other variables recorded at flush sites included (1) cover type, (2) distance to water, (3) percentage of slope, (4) distance to nearest riparian or mountain shrub cover type, and (5) cover type where flushed grouse landed (landing site).

We recorded vegetative and topographic measurements at randomly located sites to assess microhabitat availability in the cover types used most by grouse. Habitat characteristics were sampled with similar methods as described at flush sites. A total of 180 random sites were sampled during the study, 30 each month during May through July in 1984 and 1985. The number of random sites located in each cover type was based on the percentage of area occupied by that cover type in the study area. Canopy coverage and cover board readings were recorded at the origin and at points every 10 paces along a straight line until 20 readings were completed. Slope and distance to the nearest mountain shrub or riparian cover type were recorded only at the first, tenth, and twentieth frames of each random site.

Data Analysis

Data were analyzed with the Statistical Analysis System (SAS Institute, Inc. 1982). Use-availability analyses of cover types were conducted with chi-square goodness of fit tests (Neu et al. 1974) and Bonferroni z-tests (Byers et al. 1984). Data were analyzed separately for each year and pooled when differences were not significant. For analyses of canopy coverage, each plant species was placed into one of 10 categories: (1) big sagebrush, (2) low sagebrush, (3) bitterbrush, (4) other shrubs, (5) arrowleaf balsamroot, (6) other composites, (7) noncomposite forbs, (8) bluebunch wheatgrass, (9) bulbous bluegrass, and (10) other grasses. Nonparametric statistics (Mann-Whitney *U*- and Kruskal-Wallis tests) were used to analyze canopy coverage and vertical structure because these data were not normally distributed (Conover 1980). Vegetative measurements at flush sites from May through July were combined by cover type and month for comparisons with data collected at random sites for the same period. All multiple comparisons were computed with Tukey tests (Zar 1974). The Shannon-Wiener index was used to calculate plant species diversity (Hill 1973). Proportions entered into the diversity formula were derived from the total number of plant species occurrences within the frames used to estimate canopy coverage. The significance level for all tests was $P \leq .05$, and all tests of means were two-tailed. Means are followed by ± one standard deviation.

RESULTS

Home Ranges and Macrohabitat Selection

The mean size of summer home ranges was 1.87 ± 1.14 km^2 ($N = 15$, range = 36–68 locations per grouse). Based on habitats within home ranges, three trends emerged from the use-availability analysis of cover types: (1) grouse used the big sagebrush cover type more than or in proportion to availability, (2) the low sagebrush cover type was used in proportion to availability, and (3) the shrubby eriogonum and intermediate wheatgrass cover types were avoided (Table 1). These trends were similar whether use-availability was assessed within estimated home ranges or within a fixed radius around the upper and lower dancing grounds (Table 1). In addition, a single grouse from the middle dancing ground used the big sagebrush cover type more than that expected by chance within its home range and the fixed radius. Grouse were seldom found in the denser cover types, i.e., riparian and mountain shrub habitats. However, they used these cover types as escape cover in 77% of the cases where the landing site of a flushed radioed bird was observed ($N = 338$).

Microhabitat Selection

Mean distance to water did not differ significantly between flush ($\bar{x} = 297.6 \pm 183.3$ m) and random ($\bar{x} = 295.9 \pm 211.7$ m) sites ($P < .40$), and no evidence was found that Sharp-tailed Grouse sought free water. The range of slopes

TABLE 1. Summer habitat use-availability analysis showing the number of radio-tagged Columbian Sharp-tailed Grouse using the major cover types more than (+), less than (−), or in proportion to (NS)[a] that expected by chance[b], 1983–85.

	Home range				1.2-km fixed radius		
Cover types	+	−	NS		+	−	NS
Upper dancing ground							
Big sagebrush	2	0	3		0	0	5
Low sagebrush	0	1	4		0	0	5
Shrubby eriogonum	0	5	0		0	5	0
Mountain shrub	1	0	4		1	0	4
Number of grouse				$N = 5$			
Lower dancing ground							
Big sagebrush	7	0	2		8	0	1
Low sagebrush	0	3	6		0	1	8
Intermediate wheatgrass	0	2	7		0	6	3
Number of grouse				$N = 9$			
Total number of grouse				$N = 14$			

[a] Not significant.
[b] $P \leq .05$.

used by grouse was 0–47%. Grouse used three classes of slope intervals (0–9%, 10–29%, >30%) in proportion to their availability, with >95% of the use occurring on slopes <30% (Marks and Marks 1987a).

Grouse did not show a strong preference for sites that were close to mountain shrub or riparian vegetation except in 1985, the drought year. The mean distance to mountain shrub and riparian habitats measured at flush sites ($\bar{x}$ = 151.5 ± 156.5 m) was farther than that measured at random sites ($\bar{x}$ = 120 ± 99.7 m) in 1983 and 1984 (Mann-Whitney U-test $P < .04$) but significantly closer (flush sites, $\bar{x}$ = 84.4 ± 90.9 m) in 1985 ($P < .0001$).

Vertical cover measured at random sites differed significantly among cover types (Kruskal-Wallis $P < .001$). Mean cover board readings indicated that the bitterbrush cover type provided the greatest cover; big sagebrush, intermediate wheatgrass, and low sagebrush types provided intermediate cover; and eriogonum sites had very little cover (Fig. 1). A drought during 1985 resulted in significantly less vertical cover in 1985 than in 1984 (Mann-Whitney U-test $P < .01$). However, the rank order of cover availability was the same among all cover types except intermediate wheatgrass, which decreased substantially in 1985.

Eighty-three percent of the flush sites for which microhabitat measurements were taken occurred in big and low sagebrush cover types. Vegetative data on microsite use vs. availability were evaluated only for big and low sagebrush cover types because sample sizes were too small for the other types.

Vertical cover measured at flush sites differed among years within big and low sagebrush cover types (Kruskal-Wallis $P < .05$). As noted at random sites, there was significantly less cover in 1985 than in 1984. A comparison of grouse flush sites with random sites revealed that grouse selected denser cover than that measured at random sites (Fig. 1).

The cover types used most by grouse, big and low sagebrush, had a higher diversity of shrub, forb, and grass species than the other cover types (Fig. 2). The big sagebrush cover type had the highest diversity of shrubs and grasses, and the low sagebrush cover type had the highest diversity of forbs. Overall, the big sagebrush cover type had the highest structural heterogeneity (measured as the coefficient of variation of canopy coverage and cover board readings).

During 1983–85, canopy coverage of shrubs at grouse flush sites averaged about 9% in both big and low sagebrush cover types. Forb coverage averaged about 30%, and grasses ranged from 28% to 32% canopy coverage in low sagebrush and big sagebrush cover types, respectively. Overall, canopy coverage at flush sites was significantly greater than at random sites due largely to greater total forb coverage at flush sites (Table 2). Conversely, percentage of bare ground was less at flush sites than random sites in all cases (Table 2). Sites chosen by grouse in 1984 and 1985 had significantly higher arrowleaf balsamroot cover than did random sites. There was significantly higher canopy

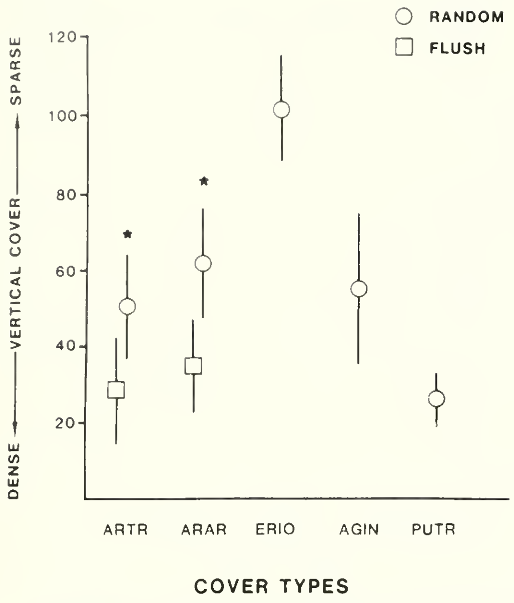

Fig. 1. Mean (± SD) cover board readings at random sites and Sharp-tailed Grouse flush sites in the major cover types (big sagebrush [ARTR], low sagebrush [ARAR], shrubby eriogonum [ERIO], intermediate wheatgrass [AGIN], bitterbrush [PUTR], 1984–85 (* = $P < .001$). Vertical axis represents the number of boxes visible on the cover board (see Methods).

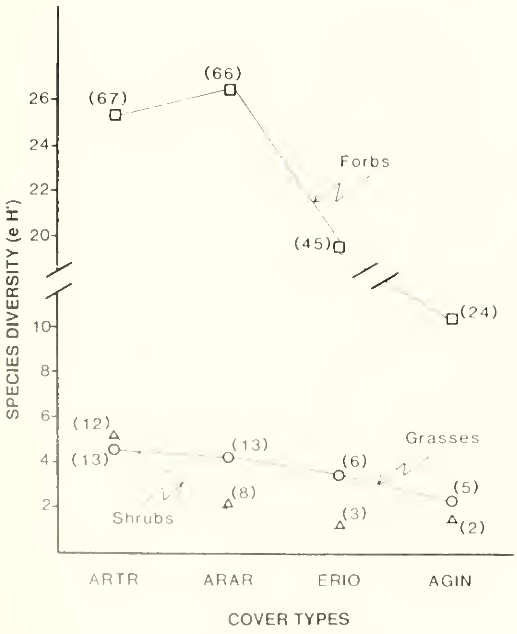

Fig. 2. Plant species diversity ($e^{H'}$) at random sites for shrubs, forbs, and grasses in the major cover types (big sagebrush [ARTR], low sagebrush [ARAR], shrubby eriogonum [ERIO], intermediate wheatgrass [AGIN]), 1984–85. The total number of plant species sampled in each cover type is in parentheses.

coverage of bluebunch wheatgrass at grouse flush sites than at random sites in the big sagebrush cover type in 1984 and in the low sagebrush cover type in 1985.

Canopy coverage at grouse flush sites in the big sagebrush type differed among years in five of six vegetative categories (Fig. 3). Bare ground increased while bulbous bluegrass, other forbs, and other composites decreased during the drought of 1985 as compared to 1983 and 1984. However, bluebunch wheatgrass increased in 1985, while the cover of arrowleaf balsamroot was not significantly different among years.

Bluebunch wheatgrass and arrowleaf balsamroot are native perennials that are considered decreaser species (Blaisdell and Pechanec 1949, Evans and Tisdale 1972); i.e., they typically decrease or are eliminated under heavy livestock grazing (Dyksterhuis 1949). Canopy coverage of decreaser forbs was significantly greater at flush sites than at random sites in the big and low sagebrush cover types (Marks and Marks 1987a).

Discussion

Summer home ranges for this subspecies in Colorado (Giesen 1987) and for other subspecies (Artman 1970, Christenson 1970, Ramharter 1976, Gratson 1983) were smaller than we observed in this study. Differences in home range size were probably a reflection of habitat condition; larger home ranges were observed in western Idaho, where decreaser forbs were limited and historic livestock grazing apparently had a greater influence on the vegetation.

From spring to fall, >90% of all grouse locations were within 1.2 km of a dancing ground. Similarly, locations of Sharp-tailed Grouse in other studies were within 1.0 and 2.5 km of dancing grounds (Pepper 1972, Oedekoven 1985, Giesen 1987, Nielsen and Yde 1982). These results suggest that maintaining habitats within 2.5 km of dancing grounds will provide summer habitat requirements for Sharp-tailed Grouse.

Compared with other cover types, big sagebrush sites had a high diversity of shrubs, forbs, and grasses; the highest structural diversity; and the greatest canopy coverage of perennial bunchgrasses. The sharptails' overall preference for the big sagebrush cover type indicated that they likely selected for habitat diversity relative to surrounding areas.

TABLE 2. Mean canopy coverage (%) of vegetative categories in big sagebrush (ARTR) and low sagebrush (ARAR) cover types at Columbian Sharp-tailed Grouse flush sites vs. random sites.

	Year							
	1984				1985			
	ARTR		ARAR		ARTR		ARAR	
Vegetative category	Flush (107)[a]	Random (42)	Flush (21)	Random (24)	Flush (107)	Random (42)	Flush (21)	Random (24)
Big sagebrush	3.43	4.03[b]	0.02	0.07	4.97	6.52[b]	0.22	0.33[b]
Low sagebrush	0.21	0.49[b]	5.45	7.84	0.55	0.79[b]	7.03	7.88
Bitterbrush	1.52	1.02	0.86	0.17	2.76	1.84[b]	1.15	0.88
Other shrubs	1.73	0.89	0.14	0.59[b]	2.21	2.69[b]	1.36	0.40
Total shrubs	6.89	6.43	6.47	8.67	10.49	11.84	9.76	9.49
Arrowleaf balsamroot	13.60	6.55[b]	12.21	3.91[b]	13.06	7.40[b]	11.91	5.28
Other composites	7.05	3.78[b]	5.14	2.95[b]	2.90	3.33	3.02	3.19
Other forbs	12.76	15.31[b]	12.83	14.24	9.70	7.87	14.97	7.22
Total forbs	33.40	25.64[b]	30.18	21.10[b]	25.66	18.60[b]	29.90	15.69
Bluebunch wheatgrass	2.93	2.56[b]	1.02	0.85	5.18	2.91	4.72	0.46[b]
Bulbous bluegrass	35.87	24.59[b]	36.83	23.09	15.97	16.52	13.20	22.33[b]
Other grasses	3.76	4.32	2.52	3.32	3.01	2.02	3.33	3.29
Total grasses	42.56	31.47	40.37	27.26	24.16	21.45	21.25	26.08[b]
Bare ground	23.93	35.93[b]	28.05	42.30[b]	40.23	48.62[b]	39.31	48.94[b]

[a] Sample size (number of transects conducted in each type).

[b] Indicates significant difference ($P < .05$) in mean canopy coverage between flush and random sites within cover types.

Shrubby eriogonum sites, which were strongly avoided by grouse, contained a low diversity of forbs, and even in the absence of grazing provided little cover. Excluding dancing grounds, Sharp-tailed Grouse studied elsewhere have exhibited similar selection against areas of sparse cover (Pepper 1972, Ziegler 1979, Klott and Lindzey 1990). The intermediate wheatgrass cover type also was avoided by grouse. Grouse were particularly absent from intermediate wheatgrass during years with relatively low numbers of grasshoppers.

Mountain shrub, riparian, and bitterbrush habitats were used primarily as escape cover during spring and summer. Beginning in late summer, mountain shrub and riparian plant species produced fruits that became an important part of the grouse diet (Marks and Marks 1987a). Proximity to this shrubby vegetation may not have been critical during early to mid-summer when the cover types preferred by grouse were providing adequate food and cover. Grouse were found closer to mountain shrub and riparian habitat than expected by chance only in the drought year (1985), when vertical cover decreased significantly in all cover types that were measured.

Sharptails apparently selected areas least modified by livestock grazing. Grouse locations were characterized by greater herbaceous cover and less bare ground than random sites. Studies of plant communities with and without grazing indicate that areas with relatively little bare ground are least modified by livestock (see

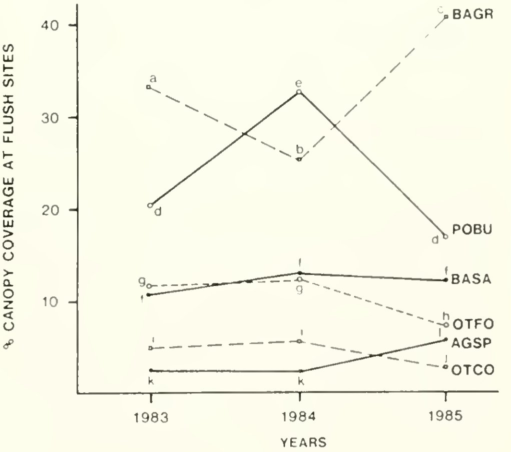

Fig. 3. Comparison of canopy coverage at Sharp-tailed Grouse flush sites in the big sagebrush cover type in western Idaho, 1983–85. On each line different letters indicate that corresponding means are significantly different at $P = .05$. (BAGR = bare ground, POBU = bulbous bluegrass, BASA = arrowleaf balsamroot, OTFO = other forbs, AGSP = bluebunch wheatgrass, OTCO = other composite forbs.)

Holechek et al. 1989). When compared with random sites, grouse locations had significantly higher proportions of forb species that decrease from overgrazing (Dyksterhuis 1949). In particular, grouse preferred microhabitats with greater abundances of arrowleaf balsamroot and bluebunch wheatgrass, two plant species that typically decline with overuse by livestock grazing (Blaisdell and Pechanec 1949, Evans and Tisdale 1972, Mueggler and Stewart 1980). These native perennials are major components of later seral stages (Hironaka et al. 1983).

The presence of arrowleaf balsamroot and bluebunch wheatgrass as cover plants during a drought year is especially noteworthy. These plants are particularly drought resistant (Tisdale and Hironaka 1981, Wasser 1982). Bulbous bluegrass, the most abundant and widespread grass in the study area, is an introduced perennial with root systems that die each year; it is virtually nonexistent during years of low moisture (Monsen and Stevens, in preparation). Indeed bulbous bluegrass contributed lower cover values in 1985 than in 1983 and 1984 (years with average moisture) (Table 2). In contrast, cover of bluebunch wheatgrass was similar among those years. In the absence of native perennials, grouse would not have had as much cover during drought years. The loss of these important cover plants may have contributed to the disappearance of Columbian Sharp-tailed Grouse from large portions of their historic range.

CONCLUSIONS AND MANAGEMENT IMPLICATIONS

Given the widespread decline of the Columbian Sharp-tailed Grouse and the fragmented nature of extant populations, conservation of all potential sources of genetic variation should be a critical concern to managers. Maintenance of shrubsteppe communities in advanced seral stages is especially important for conservation of summer habitat in the Intermountain region.

Habitat features that characterize occupied habitats in western Idaho are flat to rolling rangeland in relatively good condition with a diversity of native shrubs, forbs, and grasses. Native perennials arrowleaf balsamroot and bluebunch wheatgrass are critical for cover during a drought year. Also important is riparian vegetation and numerous patches of mountain shrubs for escape cover and late summer food. These habitat characteristics suggest that Columbian Sharp-tailed Grouse are an indicator of good range condition in the mesic shrubsteppe of the Intermountain region.

Federal land management agencies are directed to conserve candidate species and their habitats and to avoid actions that may cause the species to become listed as federally threatened/endangered. Conservation efforts for Columbian Sharp-tailed Grouse, a candidate species, must include protection and enhancement of habitats that are occupied by the subspecies throughout their range, especially disjunct populations in jeopardy of extirpation. The success of attempts to improve their current status is dependent on reducing disturbances that may damage the natural diversity of shrubsteppe habitat (e.g., overgrazing by livestock and agricultural development).

Protecting habitats within 2.5 km of dancing grounds is critical for maintainence of summer habitat. Suitable habitats for reestablishment within their historic range need to be identified. However, reestablishment efforts for this native species should not take precedence over preservation and restoration of habitats that currently support sharptails (cf. Griffith et al. 1989).

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CHARACTERISTICS OF SITES OCCUPIED BY SUBSPECIES OF *ARTEMISIA TRIDENTATA* IN THE PICEANCE BASIN, COLORADO

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Key words: Artemisia tridentata, *Colorado, sagebrush, chromatography, factor analysis, soil.*

Artemisia tridentata, big sagebrush, is the dominant plant species in the Piceance Basin of western Colorado and displays great morphological variability between sites. The existence of at least three subspecies is widely accepted (McArthur et al. 1981, 1988). These are *A. tridentata* spp. *tridentata* Beetle, *A. tridentata* spp. *wyomingensis* Beetle and Young, and *A. tridentata* spp. *vaseyana* Beetle.

Despite extensive research in the Piceance Basin (Redente and Cook 1986), we have found only one study referring to intraspecific taxa of sagebrush (Ward et al. 1985). This work referred to subspecies *tridentata* but did not indicate where this taxon was found. Because the taxa are known to respond differentially to soil and climate factors (Hironoka 1978, Sturges 1978) their existence in the basin should be recognized. The present study was designed to identify the subspecies of *Artemisia tridentata* present in the Piceance Basin and to describe soil characteristics of sites occupied by subspecies.

STUDY SITE

The Piceance Basin comprises about 3000 km^2 in Garfield and Rio Blanco counties of northwest Colorado (Fig. 1). The climate of the Piceance Basin is semiarid and shows extreme variability in monthly precipitation (Wymore 1974). Consecutive months often receive little precipitation. The mean annual precipitation for eight weather stations in the region for the period 1951–70 was 35.3 cm, with a 95% confidence interval of ±18.7 cm. About one-half of the total precipitation falls as snow. The average annual temperature ranges from 7 C at 1800 m to −1 C at 2700 m.

The strong influence of topography on temperature and precipitation results in a complex of habitats in the basin (Tiedeman and Terwilliger 1978). Generally, soil development is correlated to elevation. At higher elevations, except ridge tops, soils are dark brown, shallow mollisols. At mid-elevations, aridisols are common on deep loess. The lowest elevations are characterized by entisols developed on heavy clays and deep, sandy alluvial soils.

METHODS

Six sites dominated by sagebrush were selected for this study (Table 1). These sites spanned the environmental extremes of sagebrush habitat in the Piceance Basin. Two sites were selected from each of three broad topographic regions. High mountain sites were about 2000 m; upland terraces and valley bottom sites were below 2000 m.

Sagebrush subspecies were identified by the combined information of three techniques and verified by A. H. Winward, regional ecologist for Range and Watershed Management, USFS Intermountain Region, Ogden, Utah. The first technique involved field identification using morphological characteristics based on keys by A. H. Winward and Tisdale (1977). Leaf samples were taken for the other two procedures. Two-dimensional chromatography, as described by Hanks et al. (1973), was done on persistent overwintering leaves from three plants at each site except site 5, where the morphological variability of the sagebrush plants was greater than at the other sites. At this site five plants were

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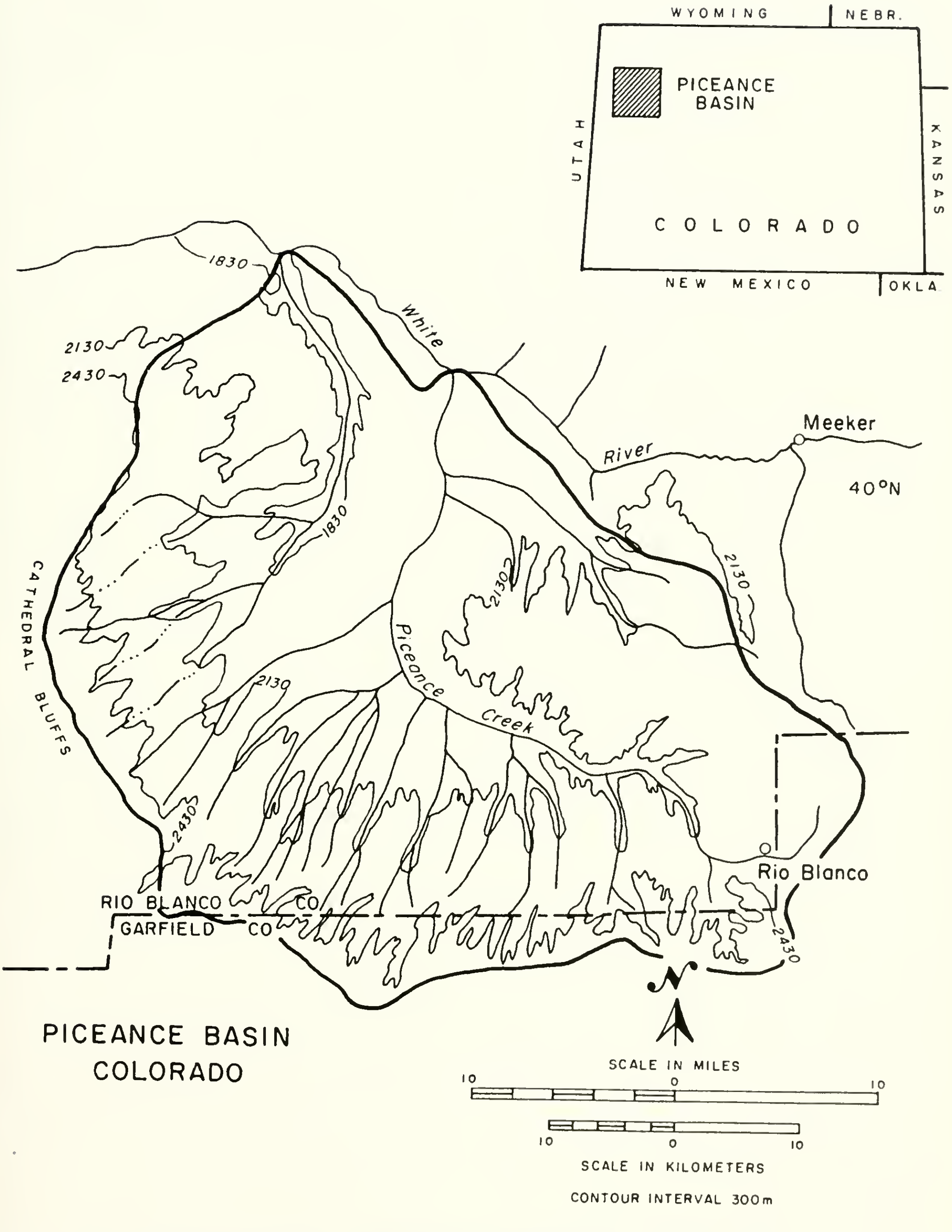
WYOMING
NEBR.
PICEANCE BASIN
UTAH
KANSAS
COLORADO
NEW MEXICO
OKLA.
1830
2130
2430
White
River
Meeker
40°N
CATHEDRAL BLUFFS
Piceance Creek
Rio Blanco
RIO BLANCO CO
GARFIELD CO
N
PICEANCE BASIN COLORADO
SCALE IN MILES
SCALE IN KILOMETERS
CONTOUR INTERVAL 300m

Fig. 1. The study area of the distribution of *Artemisia tridentata* subspecies in northwest Colorado.

tested by chromatography. Results were compared with representative chromatograms. The third procedure was a leaf extract in water. This latter method was performed on all plants tested by chromatography and on a total of approximately 18 other plants in the study sites. Leaves were crushed by hand and placed in glass containers for four hours. These were viewed under long-wave ultraviolet light and compared to descriptions by Stevens and McArthur (1974).

TABLE 1. Location, elevation, and sagebrush subspecies of study sites. VAS = ssp. *vaseyana;* TRI = ssp. *tridentata;* WYO = ssp. *wyomingensis*. Selected soil characteristics are listed for 0–15 cm and 16–30 cm soil samples for each site.

Location	Site	Elev.	ssp.	Depth in cm	% sand	% silt	pH	$CaCO^3$ est.
High mountain	1	2365	VAS	0–15	54	26	6.9	low
				15–30	52	26	6.8	low
	2	2585	VAS	0–15	40	33	6.8	low
				15–30	36	33	6.5	low
Valley bottom	3	1987	TRI	0–15	74	13	8.2	med
				15–30	67	20	8.1	med
	4	2057	TRI	0–15	56	30	8.1	med
				15–30	52	32	8.2	med
Upland terrace	5	1920	WYO	0–15	46	27	8.2	med
				15–30	51	27	8.3	med
	6	2070	WYO	0–15	32	45	7.7	med
				15–30	28	44	8.2	med

In each site, soil samples were collected at two random locations from two depths, 0–15 cm and 16–30 cm. These were analyzed for pH, organic matter, electrical conductivity, estimated $CaCO_3$, sand, silt, clay, K, Mn, Zn, Cu, P, and Fe. These data were used in a factor analysis as described by Affifi and Clark (1984). The factor scores for each site and depth were then graphed. This graph was used to interpret the axes that usually represent some environmental characteristic associated with plant species.

RESULTS

Sites 1 and 2 were high mountain sites. Sagebrush plants averaged less than 50 cm in height. Common associated plants were *Lupinus* sp., *Chrysothamnus viscidiflorus, Eriogonum umbellatum, Stipa lettermanii*, and *Symphoricarpos oreophilus*. Soils were all deeper than 40 cm and dark in color. Near these sites *Populus tremuloides* stands were common in favorable microenvironments.

Sites 3 and 4 were in a valley bottom in the Yellow Creek area. The sagebrush in these sites commonly reached heights greater than 2 m. Associated vegetation included the moss *Tortula ruralis, Chenopodium pratericola*, and *Lepidium latifolium*. Soils were light in color, and depths greater than 40 cm were common.

Sites 5 and 6 were at similar elevations to 3 and 4, but away from streams. Sagebrush plants averaged 40 cm in height. Site 5 soils were approximately 10 cm in depth. *Bromus tectorum, Gutierrezia sarothrae, Alyssum alyssoides*, and *Oryzopsis hymenoides* were the common plant species. Site 6 soils averaged 20 cm deep. Common understory species were *Koeleria cristata, Agropyron smithii*, and *Phlox hoodii*. Site 6 was surrounded by forests of *Pinus edulis* and *Juniperus osteosperma*.

Locations of *A. tridentata* subspecies in the study area relate generally to elevation. The lowest elevations supported both ssp. *wyomingensis* and ssp. *tridentata*. Factor analysis results indicate that soil texture and chemistry differences existed between the sites (Fig. 2). Subspecies *tridentata* was found in sandier soils and *wyomingensis* in siltier soils. The texture differences were generally related to topographic position. Subspecies *tridentata* was most common in valley bottoms, and ssp. *wyomingensis* was typically dominant away from streams, at the lowest elevations to approximately 2100 m. Sites above 2100 m supported ssp. *vaseyana*. Soil textures in *vaseyana* site 1 were similar to those in *tridentata* sites, while *vaseyana* site 2 textures more closely resembled those of the *wyomingensis* sites. Soil pH was lower in the *vaseyana* sites than sites with the other subspecies.

Morphological identification of ssp. *vaseyana* and *tridentata* generally agreed with the results from two-dimensional chromatography and the leaf extracts. Subspecies *wyomingensis* chromatograms were not consistently separable from those of subspecies *tridentata*. None of the *wyomingensis* chromatograms closely matched published chromatograms. Leaf extracts from ssp. *wyomingensis* showed almost no

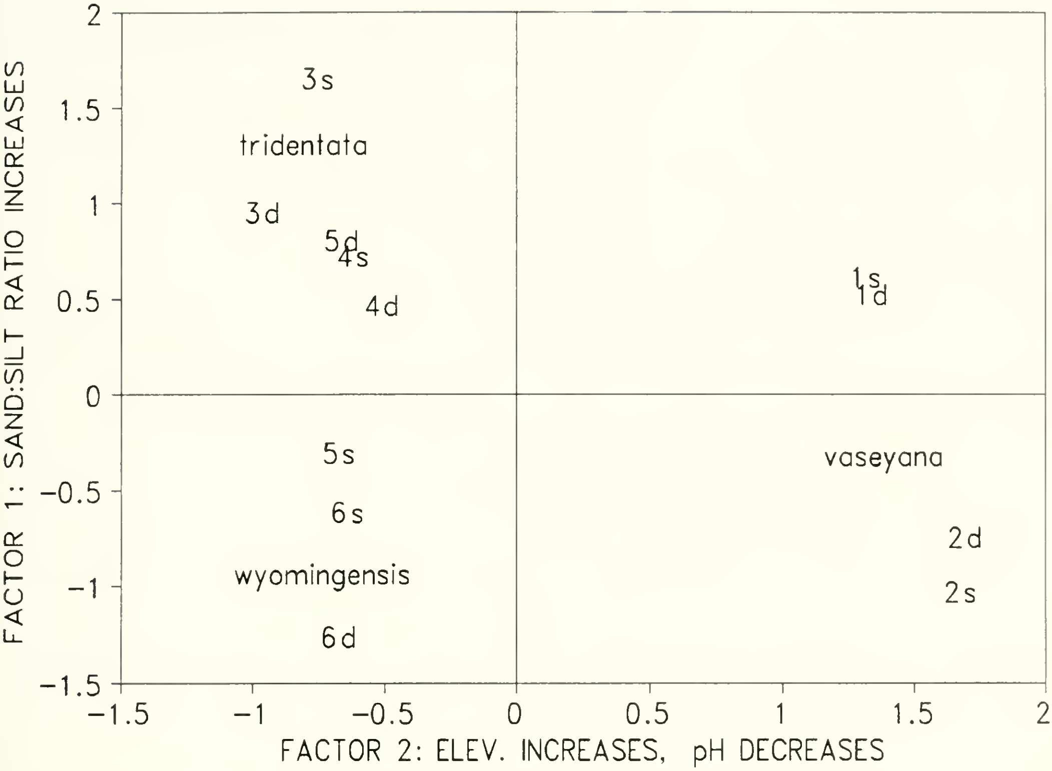

Fig. 2. Results of factor analysis on all soil data. Y axis corresponds to increasing sand:silt ratio; X axis corresponds to decreasing pH. Stand numbers are as in Table 1: s indicates sample from 0–15 cm; d indicates sample from 15–30 cm. Names show approximate region of ordination occupied by each subspecies.

fluorescence and were not separable from ssp. *tridentata*. Morphologically, however, this subspecies was separable from *vaseyana* and *tridentata* by the keys of Winward and Tisdale (1977).

DISCUSSION

Three subspecies of *A. tridentata* were identified in the Piceance Basin by reference to morphology, chromatography, and leaf extracts. The subspecies identified were *wyomingensis*, *tridentata*, and *vaseyana*. Two-dimensional chromatography and leaf extracts yielded preliminary evidence to suggest that ssp. *wyomingensis* in the Piceance Basin is chemically different from those previously identified.

The distributions of *A. tridentata* subspecies are generally related to soil moisture, temperature, depth, and parent material (Hironaka 1978). The overall tendency seems to be for ssp. *tridentata* to occupy deep, somewhat sandy soils. Although subspecies *wyomingensis* occurs in an overlapping zone with *tridentata*, it is more common in shallow, silty soils where moisture stress is greater. Subspecies *vaseyana* occurs in cool, moist sites, usually above 2100 m, but lower elevations have been documented (Goodrich et al. 1985).

Each subspecies was found at elevations and in soil textures similar to those reported in the literature. Soil texture, expressed as a ratio of sand to silt, explains the first factor in the factor analysis and distinguishes between sites of ssp. *tridentata* and *wyomingensis* (Fig. 2). That is, the vertical axis in Figure 2 corresponds to this ratio. It appears that the relative proportion of sand and silt determines whether ssp. *tridentata* or ssp. *wyomingensis* will be dominant. Barker and McKell (1983) reported similar results and suggest that the characteristics of soils associated with these subspecies are different. Fine-textured soils have been implicated in increased water stress in ssp. *wyomingensis* sites (Shumar and Anderson 1986). This might indicate a differential adaptation to water stress and, consequently, different life history strategies in the subspecies (Bonham et al. 1991).

Soils at sites with ssp. *vaseyana* are distinguished from the other sites by factor 2 of the factor analysis. This axis represents both an elevational and soil pH gradient (Table 1, Fig. 2). Sites with ssp. *vaseyana* were at a higher elevation, and soils were lower in pH and $CaCO_3$ values. The textures at these sites did not differ substantially from the other sites.

No previous study in the area has identified these taxa or characterized their habitats. The great differences in habitat preference among these subspecies suggest this is a major oversight.

ACKNOWLEDGMENTS

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USE OF LAKES AND RESERVOIRS BY MIGRATING SHOREBIRDS IN IDAHO

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Key words: shorebirds, habitat use, mudflats, water drawdown, irrigation reservoirs, migrating birds.

Shorebirds migrating long distances are vulnerable because their wetland stopover sites are limited in number and susceptible to disturbance or destruction by humans (Senner and Howe 1984, Myers et al. 1987). It is therefore critical to know which wetland areas migrating shorebirds use, and the factors making these sites attractive to shorebirds.

We conducted shorebird censuses at numerous wetland sites in Idaho with these objectives: (1) to identify types of lakes and reservoirs that are important for migrating shorebirds, (2) to identify habitat characteristics at these wetlands used by shorebirds, (3) to determine the influence of mudflat exposure and water level changes on shorebird use.

STUDY AREAS AND METHODS

A total of 19 lakes and reservoirs were censused at least once in 1989 (Table 1). Nine high-elevation lakes were visited in the Sawtooth Wilderness in early September 1976, and three high-elevation lakes in the Seafoam area of the Frank Church River of No Return Wilderness in early August 1990. Additional observations from Lake Lowell were made in 1986, 1987, and 1990. All shorebirds were censused within 100 m of the shoreline in and out of the water at all sites; thus, every 500 m of transect censused was equal to 0.1 km^2. We estimated birds per 500 m of shoreline for our density estimates. The Springfield area of American Falls Reservoir had over 15 km of mudflat exposed by drawdown during the study period and also included numerous seep areas away from the main shoreline; because of this, it was not possible to make density estimates from this site. Four of the lakes and reservoirs visited in 1989 had mudflat areas that were censused at least six times at roughly weekly intervals from mid-July to early September, the time of peak shorebird abundance in Idaho (Taylor et al. 1992). We used ANOVA and Newman-Keuls tests (Zar 1974) to compare differences in shorebird numbers at these four sites. Birds were censused by walking from 10 to 100 m back from the shoreline and using binoculars and a 25X spotting scope. Care was taken not to disturb birds. If birds moved, their numbers were kept track of, or the entire count was restarted to avoid counting birds more than once.

RESULTS

The natural lakes at high elevations we censused in 1989 (Table 2) had only 0–2 Spotted Sandpipers (see Table 3 for all scientific names). Only a single Spotted Sandpiper was found at nine high-elevation lakes visited in the Sawtooth Wilderness in September 1976. No shorebirds were found at three high-elevation lakes in the Seafoam area in early August 1990.

At the Lowell, Walcott, American Falls, and Carey areas we found significant differences in the densities of total shorebirds (ANOVA, F 2(3) 26 = 88.76, $P < .001$). Lake Lowell had significantly the most shorebirds, American Falls had significantly more than Carey Lake, but Carey Lake's higher mean was not significantly more than Lake Walcott's (Newman-Keuls, $q = 29.89$ to 7.47, for significant differences $P < .05$ or greater; $q = 2.04$, $P = .2$ for Carey Lake–Lake Walcott). These differences in shorebird numbers reflect the amount of mudflat available at the different sites; the larger the mudflats, the greater the number of shorebirds.

The pattern of more shorebirds being attracted to larger mudflats is further supported by shorebird numbers at different Lowell sites

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TABLE 1. Characteristics of Idaho lakes and reservoirs surveyed for shorebirds in 1989.

Name	County	Elevation (m)	Transect length (m)	Habitat
Reservoirs and lakes with mudflats				
American Falls	Power	1321	900	500 m mudflat
Lowell	Canyon	757	4600	1200 m mudflat
Walcott	Minidoka	1279	1500	20 m mudflat
Carey	Blaine	1453	2200	200 m mudflat
Little Camas	Elmore	1502	800	120 m mudflat
Dry	Canyon	818	1500	50 m mudflat/700 m grass
Mackay	Custer	1849	1400	200 m mudflat
Palisades	Bonneville	1708	1600	1000 m mudflat
Reservoirs and lakes without mudflats				
Cascade	Valley	1472	2600	1–2 m sandy or muddy shore
Wilson	Jerome	1224	1800	dirt or grass shore
Boulder	Valley	2127	900	2 m mud or rocky shore
Bruneau	Owyhee	763	2300	1 m mud or sandy shore
High-elevation lakes				
Alice	Blaine	2622	1000	herb or rocky shore
Toxaway	Custer	2539	900	herb or rocky shore
Edith	Custer	2611	600	herb or rocky shore
East	Valley	2373	1100	herb or rocky shore
West	Valley	2361	900	herb or rocky shore
North	Valley	2367	700	herb or rocky shore
Payette	Valley	1522	700	herb or rocky shore

responding to changes in mudflat conditions in 1989 (Fig. 1). In July Public Access No. 1 had very few shorebirds, and nearly all of its mudflats were submerged by water (Fig. 1b). The New York Canal site was submerged at this time and had no birds (Fig. 1a). When the large mudflats of the New York Canal site became exposed in August, thousands of shorebirds appeared there (Fig. 1a). Numbers of shorebirds at some of the other sites declined (Fig. 1b), which may have been due in part to birds shifting to the New York Canal site. The reflooding of Lowell in late September 1989 completely eliminated shorebirds from census areas by 27 September (Fig. 1), although American Falls Reservoir had over 500 shorebirds at this time. On 27 September 1990, with Lake Lowell very low due to dam reconstruction, there were extensive mudflats at the New York Canal site, and 926 individuals of 10 species of shorebirds were present. In early July 1986 there were hundreds of shorebirds on the exposed mudflats at Public Access No. 1, but in early July 1987, with high water flooding into riparian vegetation at this site, there were no shorebirds.

The reservoirs we counted once or a few times in 1989 usually supported the pattern of total shorebird numbers declining with decreasing mudflat size, but there were some exceptions (Table 2). Wilson, Boulder, and Cascade reservoirs all had zero or only a few meters of exposed shoreline, and they had only 1 or 2 shorebirds. Mackay Reservoir had only 2 shorebirds on 3 July when no mudflats were exposed, but 351 two weeks later when there was 200 m of mudflat. The Dry and Little Camas reservoirs supported hundreds of shorebirds (Table 2), and these sites had mudflats of 50–120 m. However, Bruneau had only 1–2 m of mud or sandy beach, and it had 79 individual shorebirds. An even stronger anomaly was Palisades, a reservoir which had exposed mudflats of about 1000 m and water drawdown continually exposing new areas, but practically no birds (Table 2).

Black-bellied Plovers, Lesser Golden-Plovers, Sanderlings, Pectoral Sandpipers, and Stilt Sandpipers were found only on mudflats with >500 m of exposed mud (Table 3). Ten other shorebirds species were most abundant at sites with >500 m of exposed mudflat. Eight shorebird species had similar-sized peaks at sites with >500 m or between 20 and 200 m of exposed mudflat. The only species with a maximum peak on mudflats between 20 and 200 m was the uncommon Long-billed Curlew. No individual shorebird species had maximum numbers at

TABLE 2. Total number and, in parentheses, density per 0.5 km of transect of shorebirds counted at lakes and reservoirs in Idaho in 1989.

Count area	N	Mean	SD	Range
Springfield	9	2296	578.1	1698–3252
American Falls	9	209	87.2	92–337
		(105)	(43.6)	(46–168.5)
Lowell	8	3061	1839.6	752–5739
		(323)	(230.6)	(78–717)
Walcott	9	54	40.6	17–153
		(18)	(13.4)	(6–50)
Carey	6	254	111.9	80–393
		(58)	(25.4)	(18–89)
Little Camas	4	294	161.5	117–446
		(184)	(101.0)	(73–279)
Dry	4	132	28	93–158
		(44)	(9.3)	(31–53)
Mackay	2	177		2–351
		(62)		(1–125)
Palisades	4	18	23.6	0–70
		(6)	(8.3)	(0–18)
Cascade	2	0		
Boulder	1	1		
		(0.6)		
Wilson	1	0		
Bruneau	1	79		
		(17)		
Alice	1	1		
		(1)		
Payette	1	0		
Edith	1	0		
Toxaway	1	1		
		(0.7)		
West	1	0		
East	1	0		
North	1	0		

sites with <5 m of mudflats or rocky/herb shorelines.

DISCUSSION

The virtual absence of shorebirds from the 19 high-elevation lakes we visited in 1976, 1989, and 1990 is similar to the findings of the only previous study of a high-elevation lake in Idaho. Visits annually to Fish Lake, Idaho Co., from 1923 to 1929 found only a few Solitary Sandpipers and Spotted Sandpipers, and one or two individuals of four other species (Hand 1932). Burleigh (1972) reported no large numbers of shorebirds at any high-elevation lakes in Idaho. Further investigation may reveal some high-elevation lakes to be important for migrating shorebirds, but the lack of mudflats at most of these lakes probably limits their use by most shorebird species.

The concentration of most shorebirds at large mudflats is consistent with our previous findings at American Falls Reservoir, where we found very few shorebirds on sandy, clay, or boulder beaches or bedrock (Taylor et al., unpublished data). Shorebirds also concentrated on mudflats at inland studies done in Nevada (Hainline 1974), Missouri (Rundle and Fredrickson 1981), and Saskatchewan (Colwell and Oring 1988), although the latter study also had some shorebird species associated with different habitats. Our study also shows that small and moderate-sized mudflats of both natural lakes and reservoirs may attract some shorebirds, especially those that often feed in water.

Shorebird species that primarily or completely feed by probing in or gleaning off land surfaces or very shallow water almost always had higher peaks on the larger mudflats, or were found there exclusively. An exception was Baird's Sandpiper, which had a similar peak between large and moderate mudflats. Five of the shorebird species with equal-sized peaks on large and moderate mudflats, the Black-necked

TABLE 3. Shorebird species found at 19 reservoirs and lakes in Idaho in 1989.

Species	Abundance[a] and habitat use[b]
Black-bellied Plover *Pluvialis squatarola*	Uncommon on large mudflats.
Lesser Golden-Plover *Pluvialis dominica*	Rare on large mudflats.
Semipalmated Plover *Charadrius semipalmatus*	Uncommon on large mudflats; rare on moderate mudflats and muddy shores.
Killdeer *Charadrius vociferus*	Common on large and moderate mudflats; uncommon on muddy shores; occasional on rocky/herb shoreline.
Black-necked Stilt *Himantopus mexicanus*	Uncommon on large and moderate mudflats; rare on muddy shores.
American Avocet *Recurvirostra americana*	Abundant on large mudflats; uncommon on moderate mudflats and muddy shores.
Greater Yellowlegs *Tringa melanoleuca*	Uncommon on large and moderate mudflats; occasional on muddy shores.
Lesser Yellowlegs *Tringa flavipes*	Common on large mudflats; uncommon on moderate mudflats; occasional on muddy shorelines.
Solitary Sandpiper *Tringa solitaria*	Occasional to rare on all shore types.
Willet *Catoptrophorus semipalmatus*	Uncommon on large mudflats; occasional on moderate mudflats; rare on muddy shorelines.
Spotted Sandpiper *Actitis macularia*	Uncommon on large and moderate mudflats, muddy shorelines; occasional on rocky/herb shorelines.
Long-billed Curlew *Numenius americanus*	Occasional on moderate mudflats; rare on large mudflats.
Marbled Godwit *Limosa fedoa*	Common on large mudflats; occasional on moderate mudflats.
Sanderling *Calidris alba*	Uncommon on large mudflats.
Semipalmated Sandpiper *Calidris pusilla*	Uncommon on large mudflats; occasional on moderate mudflats.
Western Sandpiper *Calidris mauri*	Abundant on large mudflats; common on moderate mudflats; uncommon on muddy shores.
Least Sandpiper *Calidris minutilla*	Uncommon on large mudflats; occasional on moderate mudflats.
Baird's Sandpiper *Calidris bairdii*	Common on large and moderate mudflats; occasional on muddy shores.
Pectoral Sandpiper *Calidris melanotus*	Uncommon on large mudflats.
Stilt Sandpiper *Calidris himantopus*	Rare on large mudflats.
Short-billed Dowitcher *Limnodromus griseus*	Occasional on large and moderate mudflats.
Long-billed Dowitcher *Limnodromus scolopaceus*	Common on large mudflats; uncommon on moderate mudflats and muddy shores.
Common Snipe *Gallinago gallinago*	Uncommon on large mudflats; occasional on moderate mudflats and muddy shores.
Wilson's Phalarope *Phalaropus tricolor*	Common on large and moderate mudflats; uncommon on muddy shores.
Red-necked Phalarope *Phalaropus lobatus*	Common on large and moderate mudflats; occasional on muddy shores.

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[a] A species was considered abundant if it had a single peak count over 1000 at a specific site, common with a peak over 100, uncommon with a peak over 10, occasional with a peak under 10, and rare if only one or two individuals were found.

[b] Large mudflats include American Falls, Springfield, Palisades, and Lowell, and all had water drawdown exposing mudflats of distances >500 m. Moderate mudflats include Carey, Little Camas, Dry (in part), Mackay, and Walcott, and had water drawdown exposing 20–200 m of mudflat. Muddy shores included Dry (in part), Bruneau, Cascade, Boulder, and Payette (in part), and these included small muddy shorelines or mudflats of 5 m width or less and also sandy or dirt shorelines. Rocky/herb shorelines included Alice, Dry (in part), East, Edith, North, Payette (in part), Toxaway, and Wilson

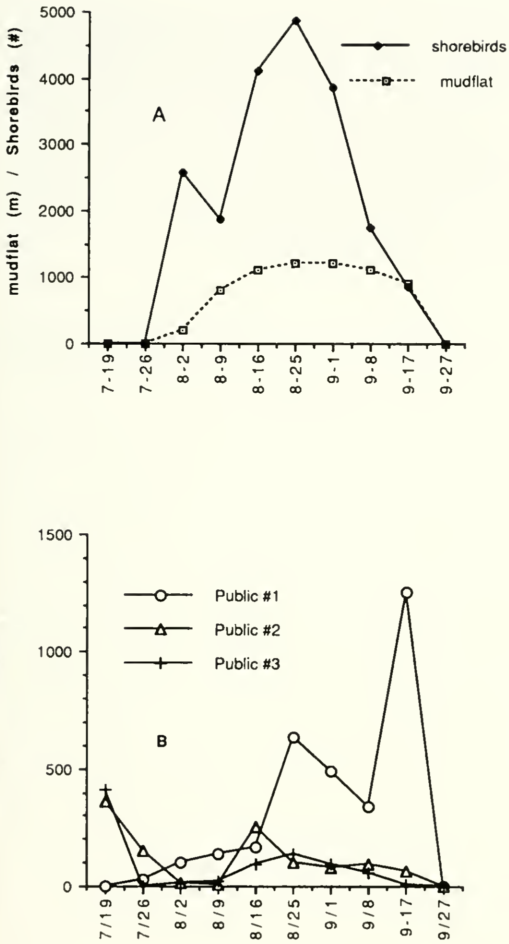

Fig. 1. Weekly counts of the total number of shorebirds at four sites at Lake Lowell, Canyon Co., Idaho, in 1989. (A) New York Canal Mouth site, with both total number of shorebirds and the amount of mudflat exposed. (B) Open circle is Public Access No. 1 site; open triangle is Public Access No. 2 site; vertical line is Public Access No. 3.

Stilt, Greater Yellowlegs, Short-billed Dowitcher, Wilson's Phalarope, and Red-necked Phalarope, along with the Long-billed Curlew, all often feed in water. The two remaining species with similar-sized peaks between large and moderate mudflats, the Killdeer and Spotted Sandpiper, were the most widespread.

This study indicates that most reservoirs and lakes in Idaho and the Intermountain West can provide habitat for shorebirds in fall migration if they have moderate to large mudflats that can be exposed by water drawdown during summer and fall. The absence of shorebirds at some reservoirs with large mudflats, in particular Palisades Reservoir in this study, indicates there are additional factors influencing shorebird use. This could include food abundance (Harrison 1982, Myers et al. 1987), which is important at American Falls Reservoir (Mihuc 1991), traditional use (Myers et al. 1987), and in the case of Palisades Reservoir possible difficulty of shorebirds locating it because it is enclosed by high mountains in all directions (personal observation). Steep-sided reservoirs, such as C. J. Strike, Hell's Canyon (personal observation), and Lower Granite Creek (Monda and Reichel 1989) on the Snake River, and stretches of the Columbia River subject to water level fluctuations (Books 1985), supported few shorebirds even with water drawdown in summer and fall.

The absence of shorebirds at Lake Lowell and Mackay Reservoir from sites when high water covered mudflats shows the importance of water drawdown exposing these areas during migration. At American Falls Reservoir we have previously found shorebird numbers to be correlated with rate of drawdown (Taylor et al., unpublished data). Water levels at reservoirs in this region are usually determined by irrigation, power generation, recreational activities such as boating, or waterfowl management. It is important that controllers of water levels at reservoirs and lakes (1) become aware of the potential or real use of shorebirds in their area and (2) manage water levels for shorebirds whenever feasible.

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DISPERSAL OF SQUARROSE KNAPWEED (*CENTAUREA VIRGATA* SSP. *SQUARROSA*) CAPITULA BY SHEEP ON RANGELAND IN JUAB COUNTY, UTAH

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Key words: Centaurea virgata *ssp.* squarrosa, *squarrose knapweed, weed dispersal, rangeland weeds, wool, sheep.*

Among *Centaurea* species naturalized in western North America, squarrose knapweed (*Centaurea virgata* Lam. ssp. *squarrosa* Gugl.) has a unique dispersal mechanism. The seeds (achenes) of other *Centaurea* species (*C. diffusa* Lam., *C. maculosa* Lam., *C. solstitialis* L., *C. jacea* L. × *C. nigra* L.) disperse either as individuals with crop seed, vehicles, and gravel, or as branches or entire plants moved by wind or vehicles, or in hay. Squarrose knapweed involucral bracts recurve or spread outward with a short terminal spine about 1–3 mm long. The entire head (capitulum) is deciduous via an abscisson layer at the base of the capitulum. Thus, the capitula of squarrose knapweed function like burs clinging to passing animals as burdock (*Arctium minus* (Hill) Bernh.), cocklebur (*Xanthium strumarium* L.), or buffalobur (*Solanum rostratum* Dunal). Soon after the discovery of squarrose knapweed in California (1950) and in Utah (1954), its occurrence was linked to the practice of trailing rangeland sheep from one area to another (Bellue 1954, Tingey 1960). On Utah rangeland squarrose knapweed is more abundant along sheep trails and on bedgrounds than in other areas (H. Gates and T. Roberts, personal communication). Wool is ideally suited to catching and holding the burlike capitula, but squarrose knapweed along trails and in sheep bedgrounds may have been carried by vehicles or other means and established in soil disturbed by sheep. The objective of this study was to determine if the distribution of squarrose knapweed in Utah is due to seed carried in the wool of rangeland sheep.

METHODS AND MATERIALS

In mid-April 1990, sheep examined in this study were trailed from winter range west of Tintic Junction, Juab County, Utah, and sheared before being moved to spring range. We received permission from the owners to collect wool samples during shearing of a band that had wintered on rangeland known to have squarrose knapweed. We had predicted that sheep would pick up the "burs" by lying on or brushing against knapweed plants growing on their bedgrounds. However, we saw no obvious knapweed capitula in belly wool or on the sides of sheep being sheared. One shearer pointed out several ewes with a profusion of knapweed capitula around their faces and on top of their heads (Fig. 1). We then collected samples of topknot wool (that shorn from the top of the head) from 458 randomly selected white ewes from a band of approximately 2500 ewes at the Jericho shearing station in Juab County, Utah. Black ewes were not sampled. Samples from individual ewes, averaging 10 g, were kept separate in small plastic bags. Squarrose knapweed capitula were sorted by hand from each sample, and the number of achenes per capitulum was recorded. Filled achenes (hard, plump, dark tan or brown achenes) and light achenes (softer, flatter, pale tan or whitish achenes) were recorded separately. Presence or absence of insect galls (*Urophora affinis* Frauenfeld and *U. quadrifasciata* [Meigen]) in the knapweed capitula was noted.

Achene viability was determined with germination trials run for 10 days at 20 C, 12 hours

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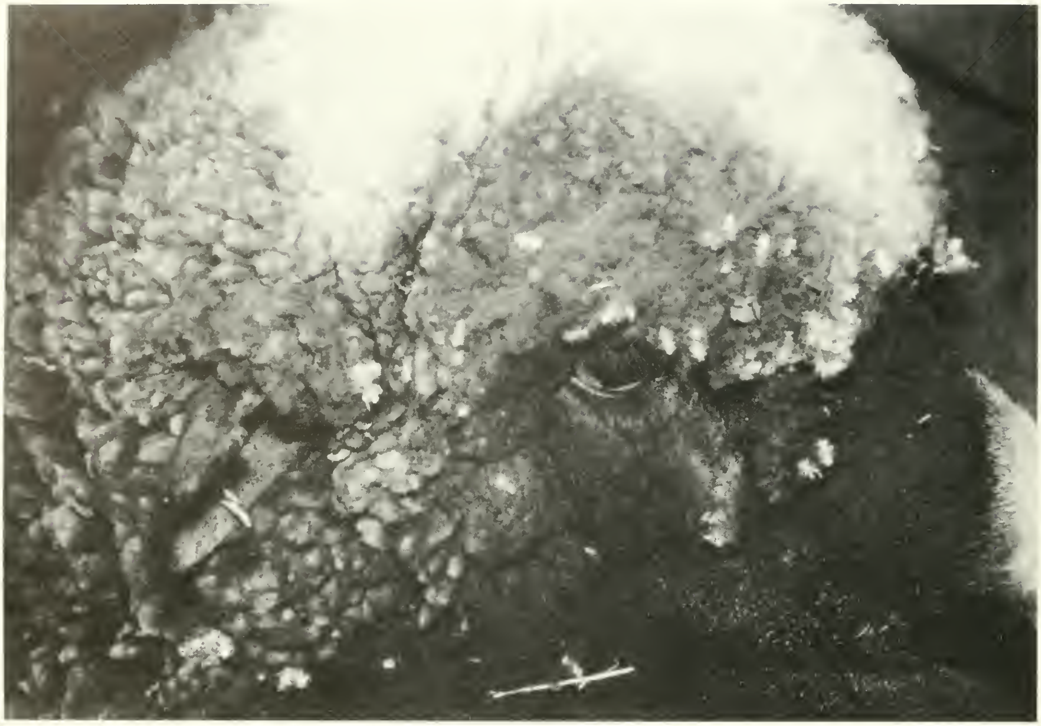

Fig. 1. Numerous squarrose knapweed capitula were caught as burs in the topknot wool of sheep that had wintered where squarrose knapweed occurred on rangeland in Juab County, Utah.

TABLE 1. Proportion of capitula containing 0–6 achenes per capitulum, comparing all capitula from an intact plant with sheep-gathered capitula removed from topknot wool, in Juab County, Utah.

Achenes/capitulum	Intact plant %	Extracted from wool %
0	14	75
1	12	18
2	19	6
3	35	1
4	17	trace
5	3	0
6	trace	0

light alternating with 12 hours dark. Seeds were placed in germination boxes on wetted blotter paper. Filled and light achenes were tested separately. We germinated 30 filled achenes in four replications in each of two trials. Two trials of light achenes were run with 20 seeds in each of two replications.

In August 1989, a squarrose knapweed plant with all of its capitula was collected in a bag. We dissected the capitula and recorded the number of achenes per capitulum. These values were compared to capitula and achenes found on sheep.

RESULTS

We determined that sheep on rangeland infested with squarrose knapweed picked up and carried its burlike capitula. Squarrose knapweed capitula were present in topknot wool samples from 73% of the ewes. A total of 2469 knapweed capitula were recovered from the 458 ewes, an average of 5.5 capitula per 10 g wool. Most capitula were on the wool surface, although a few were embedded deeply and appeared to have been there longer as they were saturated with lanolin and spines had worn off the involucral bracts.

Seventy-five percent of the sheep-gathered capitula were barren, compared with 14% of the capitula produced on a whole plant (Table 1). Only 49% of the wool samples that contained capitula had one or more achenes. Barren capitula in this study were not the result of biocontrol insects because we found no insect galls.

The number of knapweed capitula on sheep

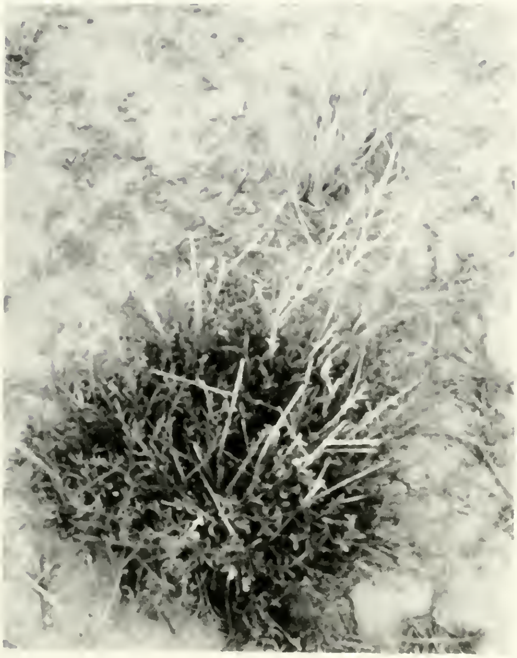

Fig. 2. Squarrose knapweed plants along the sheep trails west of the Jericho shearing station were grazed in mid-April 1990. A few capitula remain on the upper right side of the plant.

heads would lead a casual observer to conclude that the sheep carry more achenes than we found by dissecting the capitula. Among all ewes sampled, only 36% carried achenes in the sampled topknot wool. These seed-carriers averaged 4.5 filled achenes per 10 g wool. Those filled achenes averaged 69% germination. In addition to the filled achenes, 5% of the light achenes germinated. Light achenes composed only 23% of the total number of achenes.

DISCUSSION

Sheep carried squarrose knapweed capitula but not as many achenes as the number of capitula would indicate if the proportion were the same as that estimated in August. This finding could indicate one of two conditions: (1) the capitula were picked up in late winter or early spring, when only the lighter capitula remained on the plants, or (2) some achenes were lost from capitula lodged in the wool during late summer or fall. In late summer heavier capitula are more easily dislodged from plants than are the lighter capitula. Capitula do not open widely at maturity; instead, achenes sift out through a small opening created as the dried flowers fall from the capitulum. The proportion of empty capitula increases with time following maturity as plants are shaken by wind, animals, or vehicles.

Sheep acquired knapweed capitula in a manner different from what we had predicted. Although some capitula clung to sheep brushing against plants or lying upon them, the numerous knapweed capitula in the wool around their faces suggest that ewes searched out squarrose knapweed as a food source. We observed that squarrose knapweed plants along the sheep trails had been grazed (Fig. 2). This relationship was mutually beneficial for knapweed and sheep, providing propagule dispersal for the knapweed and nourishment for the sheep.

Previously reported to be poor forage (Tingey 1960), squarrose knapweed rosette leaves may be an excellent source of protein in late winter and early spring. Nutrient content of spotted knapweed rosette leaves is comparable to native forage plants with 9–18% crude protein (Kelsey and Mihalovich 1987). Similar values have been obtained for diffuse knapweed and yellow starthistle rosette leaves (Roché, unpublished data). In the study area, September 1989 through May 1990 was unusually dry (Utah State University Tintic research site weather station, unpublished data), and the normal growth of cheatgrass (*Bromus tectorum* L.) was not present on the winter range. Squarrose knapweed, a deep-rooted perennial forb, was one of the few plants exhibiting new growth at the time sheep would normally forage on cheatgrass.

Although we found that sheep carry squarrose knapweed seeds as they move across rangeland, they are by no means the only dispersal mechanism for squarrose knapweed. Other animals, both domestic and wild, may carry knapweed seeds. In addition, these rangelands are heavily used by off-road vehicle recreationists. Mining traffic, railroad activity, and military maneuvers are important in certain areas. Hunters, rockhounds, and other recreationists also frequent the area.

Shearing limits the dispersion of squarrose knapweed by sheep. It is unlikely that knapweed achenes remained on sheep after shearing. These ewes had not yet lambed, and so all sheep in this band left the knapweed-infested winter range shorn of seeds. Seeds in the wool are removed at the woolen mill, which has been one of the fates of squarrose knapweed seed for centuries, as evidenced by squarrose knapweed found at Juvénal Gate, a woolen mill in France where imported wool was washed for 200 years, beginning in 1686 (Thellung 1912).

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VEGETATION ASSOCIATED WITH TWO ALIEN PLANT SPECIES IN A FESCUE GRASSLAND IN GLACIER NATIONAL PARK, MONTANA

Robin W. Tyser[1]

Key words: alien flora, Glacier Park, Festuca *grasslands.*

The presence of alien flora in natural area grasslands of the Great Basin and surrounding areas is of considerable concern, given the widespread success of alien flora and associated decline of native species in this region (Young et al. 1972, Mack 1986, 1989). Surveys of indigenous bunchgrass communities in northern Rocky Mountain national parks have detected the occurrence of several alien plant species (Koterba and Habeck 1971, Stringer 1973, Weaver and Woods 1985, 1986, Tyser and Worley 1992). In addition, alien species have commonly been used to revegetate human-disturbed sites such as roadsides and housing areas in national parks. Livestock-related introduction of Eurasian pasture grasses by private outfitters is also known to have occurred (Glacier National Park Records 1939). However, in spite of these observations and practices, the effects of alien vegetation in natural area grasslands of this region remain poorly studied.

This study compares the indigenous vascular flora and cryptogamic ground cover associated with two alien species, *Centaurea maculosa* Lam. (spotted knapweed) and *Phleum pratense* L. (common timothy), that have invaded a fescue grassland in Glacier National Park, Montana. *C. maculosa,* now a noxious rangeland invader throughout the Pacific Northwest (Watson and Renney 1974, Lacey 1989), was first detected in the park in the mid-1960s (R. Wassem, personal communication). Earlier observations have shown that this species is expanding into grasslands adjacent to roadsides in the park and reducing species richness (Tyser and Key 1988). The impact of *C. maculosa* on the cryptogamic ground crust—of potential importance in soil stabilization, moisture retention, and nitrogen fixation (Rychert and Skujins 1974, Anderson et al. 1982, Brotherson and Rushforth 1983)—has not yet been considered, nor has the impact of *C. maculosa* been compared to that of other alien species. *P. pratense* is widely distributed throughut the park's grasslands. Unlike *C. maculosa,* this species appears to have been intentionally seeded in grasslands by outfitters before the 1940s and along roadsides by park personnel before the 1980s (D. Lange and J. Potter, personal communication).

STUDY SITE AND METHODS

The ca 10-ha study area, located adjacent to Going-to-the-Sun Highway in the St. Mary drainage of Glacier National Park, Montana, is fairly topographically homogeneous, i.e., clearly defined drainage channels are absent, and slope, exposure, and substrate texture are relatively uniform. The study area includes a large (ca 5 ha), irregularly shaped stand dominated by *Phleum pratense* and a small (ca 0.1 ha) stand adjacent to the roadside ditch dominated by *Centaurea maculosa.* The *Centaurea* stand extends >20 m away from the ditch and is not part of the road-cut corridor. The remaining portion of the study site is composed of a stand of native *Festuca* grasses and associated vegetation in which invasion by alien species has been minimal. Though no homesteading is known to have occurred in the study area before establishment of the park in 1910, this area was likely used as summer pasture for concession trail horses from approximately 1915 to 1940 (B. Fladmark, personal communication). The study area has not been used for stock grazing since that time. Otherwise, there is no indication that any of the areas sampled in the three stands have been subjected to anthropogenic disturbance since the park was established. In addition, no fires have been recorded in or near the study area since 1910. A cryptogam ground layer composed of small lichens and mosses covering undisturbed soil surfaces is commonly present. Qualitative observation suggests that mosses are the dominant element in this layer. Mean annual precipitation in the study area is ca 65 cm (Finklin 1986).

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In each stand, vegetation was sampled using 20 × 50-cm quadrat frames along two transects placed in representative areas. Within each quadrat, presence of all vascular species was determined, and the canopy cover of each vascular species and the surface cover of the cryptogamic ground crust were estimated to the nearest percentage. A stratified random sampling procedure was used in which quadrats were randomly placed along transect segments of fixed length. For the *Centaurea* stand, transects were 20 m long, and one quadrat was randomly placed within each 2-m segment (N = 20 quadrats). For the *Phleum* and *Festuca* stands, transects were 100 m long, and one quadrat was randomly placed within each 5-m segment (N = 40 quadrats per stand).

Five vegetation measures were calculated for each individual quadrat: (1) vascular species cover diversity using the Shannon-Wiener index ($H' = -\Sigma p_i \log p_i$), (2) vascular species richness, (3) cumulative canopy cover of native forb species, (4) cumulative canopy cover of native grass species, and (5) surface cryptogam cover. One-way ANOVAs were used to assess among-stand differences for each of these quadrat measures. With the exception of the diversity measures, data did not meet parametric assumptions (normal distributions, homogeneous variances) and could not be transformed using standard logarithmic, arcsine, or square root transformations. Therefore, data were analyzed by the Kruskal-Wallis nonparametric one-way ANOVA procedure as described by Conover and Iman (1983). The Tukey multiple comparison procedure, applicable to both parametric and nonparametric ANOVAs (Conover and Iman 1981), was used to make pair-wise among-stand comparisons. Species nomenclature follows that of Hitchcock and Cronquist (1973).

RESULTS AND DISCUSSION

Prominent graminoid and forb species in the *Festuca* stand included *Achillea millefolium, Carex spp., Festuca idahoensis, F. scabrella, Gaillardia aristata,* and *Lupinus sericeus* (Table 1). Species composition of this stand was similar to prairie communities described elsewhere in the Pacific Northwest, e.g., the *Festuca scabrella/F. idahoensis* association of western Montana (Mueggler and Stewart 1980), the *Festuca/Danthonia* prairie of Alberta (Stringer 1973), and the Washington Palouse prairie (Daubenmire 1970). Estimated surface cover of the cryptogam layer in this stand was relatively high, characteristic of western bunchgrass prairies (Daubenmire 1970, Mack and Thompson 1982). Three alien species were sampled within the *Festuca* stand, though total cover of these species was <1.0%.

Significant among-stand variation occurred for all community measures (Table 2). Each of these measures was lowest in the *Centaurea* stand. Canopy cover of native forbs and cryptogam ground cover in this stand were particularly low, only ca 18% and 4%, respectively, of the corresponding *Festuca* stand measures. Thus, effects of the *Centaurea maculosa* invasion on the native flora in the study site appear to be relatively severe. The impact of this species is even more impressive considering its relatively recent entry into the park.

All but one of the *Phleum* stand measures were significantly lower than those of the *Festuca* stand (Table 2). Canopy cover by native graminoids in the *Phleum* stand was reduced to about 50% of its level in the *Festuca* stand. However, forb cover differences between these two stands were not statistically significant (Table 2). Three species (*Achillea millefolium, Agoseris glauca,* and *Lupinus sericeus*) were among the four forb species with highest canopy cover in each stand, suggesting that the forb components of these two stands were relatively similar. These observations suggest that *Phleum* invasion has affected native graminoids more than native forbs. It should also be noted that while mean quadrat richness was lower in the *Phleum* stand (Table 2), eight more species were recorded in this stand than in the *Festuca* stand (N = 59 vs. N = 51; see Table 1). Thus, different *Phleum* vs. *Festuca* richness patterns may occur if comparisons are derived from sampling units larger than the 0.1-m^2 quadrats used in this study.

Cryptogam cover in the *Phleum* stand was approximately 50% lower than in the *Festuca* stand (Table 2). Mack and Thompson (1982)

TABLE 1. Canopy cover (%) estimates of species within the *Festuca*, *Phleum*, and *Centaurea* stands. ° = alien species.

Species	*Festuca*	*Phleum*	*Centaurea*
GRAMINOIDS			
Agropyron caninum	0.4	0.6	
Agropyron spicatum	0.3	0.3	
Carex spp.	12.3	5.6	9.3
Danthonia intermedia	4.2	0.9	
Festuca idahoensis	9.2	4.3	0.2
Festuca scabrella	7.1	4.1	2.1
Helictotrichon hookeri	0.9	<0.1	
Koeleria cristata	1.4	0.4	<0.1
Phleum pratense°	0.2	38.4	0.7
Poa juncifolia		<0.1	
Poa pratensis°	<0.1	0.9	1.0
Stipa occidentalis	3.7	2.1	
Stipa richardsonii	0.1	0.8	
FORBS			
Achillea millefolium	11.7	8.6	0.8
Agoseris glauca	4.0	4.3	
Allium cernuum	0.1	<0.1	
Amelanchier alnifolia	0.3	0.9	0.5
Androsace septentrionalis	1.0	0.3	
Anemone multifida	1.4	1.0	<0.1
Antennaria microphylla	0.8	0.3	1.7
Arabis glabra		<0.1	
Arabis nuttallii	0.2	0.1	<0.1
Arctostaphylos uva-ursi	0.4	0.2	
Aster laevis		1.8	0.9
Berberis repens	0.1	0.6	0.3
Campanula rotundifolia	0.5	1.0	<0.1
Castilleja cusickii	0.3	<0.1	
Centaurea maculosa°			62.0
Cerastium arvense	4.0	3.1	0.7
Collomia linearis		<0.1	
Comandra umbellata	0.5	0.3	
Epilobium angustifolium		0.5	
Erigeron subtrinervis		1.5	
Erysimum inconspicuum		0.3	
Fragaria virginiana	<0.1	0.7	
Gaillardia aristata	1.9	0.6	<0.1
Galium boreale	0.6	1.8	0.2
Gentiana amarella	1.3	0.7	
Geranium viscosissimum	<0.1	1.2	
Hedysarum boreale	0.5		
Heuchera cylindrica	0.1	0.2	0.2
Hieracium umbellatum			0.2
Juncus balticus		1.0	
Lathyrus ochroleucus		0.2	
Lithospermum ruderale	1.9	3.9	0.7
Lomatium triternatum	1.0	2.4	0.3
Lupinus sericeus	5.6	6.0	<0.1
Monarda fistulosa		0.6	
Orthocarpus tenuifolius	1.2	<0.1	
Oxytropis campestris	2.8	0.9	
Oxytropis splendens	0.3		
Penstemon confertus	0.8	1.9	0.7
Potentilla arguta	<0.1	1.1	
Potentilla gracilis	<0.1	0.4	0.3
Potentilla hippiana	0.5		
Prunus virginiana		0.1	
Rhinanthus crista-galli	0.9	0.4	
Rosa woodsii	1.3	2.3	0.2
Silene parryi	0.4	0.1	<0.1
Sisyrinchium angustifolium	0.2	0.4	
Solidago missouriensis	1.6	1.8	0.2
Taraxacum officinale°	0.2	1.4	0.3
Tragopogon dubius°	<0.1	0.4	
Vicia americana		1.6	1.0
Zigadenus venenosus	<0.1		

TABLE 2. Among-stand comparisons of quadrat means for five vegetation measures. N = 40, 40, and 20 quadrats, respectively, for the *Festuca*, *Phleum*, and *Centaurea* stands.

	H'	Richness	Native graminoids	Native forbs	Cryptogam crust
Festuca°	0.966^{a}	14.8^{a}	39.5^{a}	48.4^{a}	28.9^{a}
Phleum	0.872^{b}	12.9^{b}	19.2^{b}	55.1^{a}	15.1^{b}
Centaurea	0.385^{c}	7.2^{c}	11.6^{c}	8.8^{b}	1.3^{c}
$F_{2,97}$	90.084	41.150	53.807	40.896	31.835
P	<.001	<.001	<.001	<.001	<.001

°Within each vegetation measure, means with different letters differ significantly from one another ($P < .05$, Tukey multiple comparison tests).

suggest that the extensive rhizome-tiller mats of Eurasian grasses limit cryptogam colonization sites, which may account for the reduced cryptogam cover observed in the *Phleum* stand. A large elk herd overwinters in the St. Mary valley grasslands in which the study area was located (Martinka 1983). Thus, it is possible that elk trampling/grazing may reduce cryptogam cover and facilitate *Phleum* invasion.

The role played by pre-1940 horse grazing in the occurrence of *Phleum* in the study site cannot be assessed. However, the prominence of this species some 50 years after the cessation of horse grazing does indicate that ongoing livestock grazing is not necessary for its persistence. The more recent *Centaurea maculosa* invasion in the study site and in other fescue grasslands in the park (Tyser and Key 1988, Tyser and

Worley 1992) suggests that livestock grazing is not a prerequisite for successful invasion of natural areas by this species. The success of both *P. pratense* and *C. maculosa* in the study site suggests that mechanisms proposed for the success of alien flora in agro-systems, e.g., rapid colonization of disturbed sites, structural and physiological adaptations to grazing and trampling, and low palatability (Mack and Thompson 1982 and references therein, Lacey et al. 1986, Locken and Kelsey 1987, Kelsey and Bedunah 1989), may also operate in natural area systems. In addition to overwintering elk, diggings of other native herbivores, especially ground squirrels (*Spermophilus columbianus*), were common throughout the study area. At any rate, though the status and impacts of *C. maculosa* and *P. pratense* require additional research, this study shows that the potential effects of these species—particularly that of *C. maculosa*—in natural area bunchgrass prairies need to be seriously contemplated.

Reduction of *Phleum pratense* is not a realistic option in Glacier National Park or other natural areas in which this species is now widely established. Perhaps the most reasonable recommendation for this species and other Eurasian grasses is simply that resource managers not use these species for revegetation (see also Wilson 1989). *Centaurea maculosa*, though potentially more ecologically disruptive than *P. pratense*, is at an earlier stage of invasion in the park and probably in other natural areas in this region as well. Thus, the fate of this species may yet be influenced by appropriate resource management actions.

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PLANT ADAPTATION IN THE GREAT BASIN AND COLORADO PLATEAU

Jonathan P. Comstock[1] and James R. Ehleringer[1]

ABSTRACT—Adaptive features of plants of the Great Basin are reviewed. The combination of cold winters and an arid to semiarid precipitation regime results in the distinguishing features of the vegetation in the Great Basin and Colorado Plateau. The primary effects of these climatic features arise from how they structure the hydrologic regime. Water is the most limiting factor to plant growth, and water is most reliably available in the early spring after winter recharge of soil moisture. This factor determines many characteristics of root morphology, growth phenology of roots and shoots, and photosynthetic physiology. Since winters are typically cold enough to suppress growth, and drought limits growth during the summer, the cool temperatures characteristic of the peak growing season are the second most important climatic factor influencing plant habit and performance. The combination of several distinct stress periods, including low-temperature stress in winter and spring and high-temperature stress combined with drought in summer, appears to have limited plant habit to a greater degree than found in the warm deserts to the south. Nonetheless, cool growing conditions and a more reliable spring growing season result in higher water-use efficiency and productivity in the vegetation of the cold desert than in warm deserts with equivalent total rainfall amounts. Edaphic factors are also important in structuring communities in these regions, and halophytic communities dominate many landscapes. These halophytic communities of the cold desert share more species in common with warm deserts than do the nonsaline communities. The Colorado Plateau differs from the Great Basin in having greater amounts of summer rainfall, in some regions less predictable rainfall, sandier soils, and streams which drain into river systems rather than closed basins and salt playas. One result of these climatic and edaphic differences is a more important summer growing season on the Colorado Plateau and a somewhat greater diversification of plant habit, phenology, and physiology.

Key words: cold desert, plant adaptation, water stress, phenology, salinity, Great Basin, Colorado Plateau.

Several features arising from climate and geology impose severe limitations on plant growth and activity in the Great Basin and Colorado Plateau. The climate is distinctly continental with cold winters and warm, often dry summers. Annual precipitation levels are low in the basins, ranging from 100 to 300 mm (4–12 inches), and typically increasing with elevation to 500 mm (20 inches) or more in the montane zones. Precipitation levels are lowest along the southwestern boundary of the Great Basin in Nevada and increase both to the north and east, and to the southeast moving into the Colorado Plateau (Fig. 1, Table 1). The fraction of annual precipitation during the hot summer months (June–September) varies considerably, from 10–20% in northern Nevada to 30–40% along the boundary of the Cold and Mojave deserts in southwestern Nevada and southern Utah, and 35–50% throughout much of the Colorado Plateau. Winter precipitation falls primarily as snow in the Great Basin and higher elevations

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TABLE 1. Selected climatic data for low-elevation sites in different regions of the Great Basin, Mojave Desert, and Colorado Plateau. Values are based on averages for the U.S. Weather Bureau stations indicated. The three divisions of the year presented here reflect ecologically relevant units, but are unequal in length. The five months of October–February represent a period of temperature-imposed plant dormancy and winter recharge of soil moisture. The spring months of March–May represent the potential growing period at cool temperatures immediately following winter recharge. The summer and early fall from June through September represent a potential warm growing season in areas with sufficient summer rain or access to other moisture sources.

				Total precipitation				Mean temperature			
Region	Map # (Fig. 1)	Weather station	Elevation (m)	Annual (mm)	Oct-Feb (%)	Mar-May (%)	Jun-Sep (%)	Annual (°C)	Oct-Feb (°C)	Mar-May (°C)	Jun-Sep (°C)
Northern Great Basin	1	Fort Bidwell	1370	402	63	24	13	9.0	3.0	8.0	17.3
	2	Reno	1340	182	61	24	15	9.5	3.3	8.4	18.0
	3	Elko	1547	230	52	29	19	7.6	0.1	7.1	17.5
	4	Snowville	1390	300	43	33	24	7.4	0.7	6.2	18.4
Southern Great Basin	5	Sarcobatus	1225	85	45	22	33	13.5	6.4	12.5	23.1
	6	Caliente	1342	226	47	24	29	11.7	4.1	11.2	21.5
	7	Fillmore	1573	369	44	34	22	11.0	3.0	10.0	21.7
Mojave Desert	8	Trona	517	102	70	19	11	19.0	11.3	18.4	29.0
	9	Beaverdam	570	169	50	23	28	18.3	11.0	16.9	28.6
Colorado Plateau	10	Hanksville	1313	132	36	19	45	11.4	2.1	11.5	22.8
	11	Grand Junction	1478	211	39	25	36	11.3	2.4	10.9	22.9
	12	Blanding	1841	336	48	19	33	9.7	2.1	8.7	19.9
	13	Tuba City	1504	157	38	21	41	12.6	4.8	12.0	22.8
	14	Chaco Canyon	1867	220	35	20	45	10.3	2.6	9.4	20.6

of the Colorado Plateau, which is thought to be a critical feature ensuring soil moisture recharge and a reliable spring growing season (West 1983, Caldwell 1985, Dobrowolski et al. 1990). During the winter period, precipitation is generally in excess of potential evaporation, but low temperatures do not permit growth or photosynthesis, and exposed plants may experience shoot desiccation due to dry winds and frozen soils (Nelson and Tiernan 1983). Strong winds can also cause major redistributions of the snowpack, sometimes reversing the expected increase in precipitation with elevation and having important consequences to plant distributions (Branson et al. 1976, Sturges 1977, West and Caldwell 1983). The important growing season is the cool spring when the soil profile is recharged from winter precipitation; growth is usually curtailed by drying soils coupled with high temperatures in early or mid-summer. A clear picture of this climatic regime is essential to any discussion of plant adaptations in the region.

A second major feature affecting plant performance is the prevalence of saline soils caused by the combination of low precipitation and the internal drainage typical of the Great Basin. In this paper we address the salient morphological, physiological, and phenological specializations of native plant species as they relate to survival and growth under the constraints of these potentially stressful limitations. We emphasize (1) edaphic factors, particularly soil salinity and texture, and (2) the climatic regime ensuring a fairly dependable, deep spring recharge of soil moisture despite the overall aridity, as factors molding plant adaptations and producing the unique aspects of the regional plants and vegetation. The majority of the Great Basin lies at moderately high elevations (4000 ft and above), and it is occupied by cold desert plant communities. Reference to "the Great Basin" and its environment in this paper will refer to this high-elevation region as distinct from that corner of the Mojave Desert that occupies the southwestern corner of the Great Basin geographic unit (Fig. 1). Our emphasis will be placed on these cold desert shrub communities in both the Great Basin and the Colorado Plateau ranging from the topographic low points of the saline playas or canyon bottoms up to the pinyon-juniper woodland. The lower-elevation, warmer,

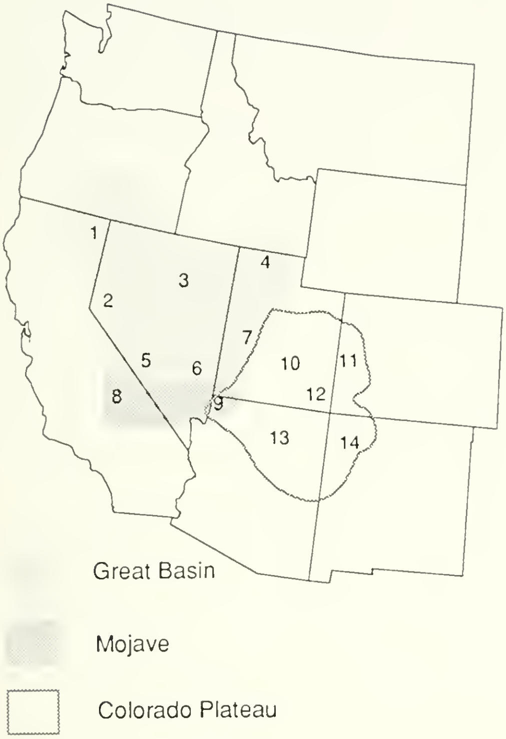

Fig. 1. Distribution of the major desert vegetation zones in the Great Basin and Colorado Plateau. Numbers indicate locations of climate stations for which data are presented in Table 1. Most of the Mojave Desert indicated is geologically part of the Great Basin, but, due to its lower elevation and warmer temperatures, it is climatically distinct from the rest of the region.

and drier Mojave Desert portion of the Great Basin will be considered primarily as a point of comparison, and for more thorough coverage of that region we recommend the reviews by Ehleringer (1985), MacMahon (1988), and Smith and Nowak (1990). For the higher montane and alpine zones of the desert mountain ranges, the reader is referred to reviews by Vasek and Thorne (1977) and Smith and Knapp (1990). We are indebted in our own coverage of the cold desert to other recent reviews, including Caldwell (1974, 1985), West (1988), Dobrowolski et al. (1990), and Smith and Nowak (1990).

The Great Basin and the Colorado Plateau share important climatic features such as overall aridity, frequent summer droughts, and continental winters; yet they differ in other equally important features. Temperatures on the Colorado Plateau are similar to equivalent elevations in the southern Great Basin, but summer precipitation is substantially greater on the Colorado Plateau (Table 1). Soils and drainage patterns also differ in crucial ways. The highlands of the Colorado Plateau generally drain into the Colorado River system. In many areas extensive exposure of marine shales from the Chinle, Mancos, and Morrison Brushy-Basin formations weather into soils that restrict plant diversity and total cover due to high concentrations of $NaSO_4$, and the formation of clays that do not allow water infiltration (Potter et al. 1985). In other areas massive sandstone outcrops often dominate the landscape. Shrubs and trees may root through very shallow rocky soils into natural joints and cracks in the substratum. Deeper soils are generally aeolian deposits forming sands or sandy loams. In contrast, high elevations of the Great Basin drain into closed valleys and evaporative sinks. This results in greater average salinity in the lowland soils of the Great Basin, with NaCl being the most common salt (Flowers 1934), and a more extensive development of halophytic or salt-tolerant vegetation. Soils tend to be deep, especially at lower elevations, and vary in texture from clay to sandy loams. Summer-active species with different photosynthetic pathways, such as C_4 grasses and CAM succulents, are poorly represented in much of the Great Basin, but the combination of increased summer rain, sandier soils, and milder winters at the lower elevations of the Colorado Plateau has resulted in a greater expression of phenological diversity.

The interactions of edaphic factors and climate are complex and often subtle in their effects on plant performance. Furthermore, plant distributions are rarely determined by a single factor throughout their geographic range, even though a single factor may appear to control distribution in the context of a local ecosystem. Species-specific characteristics generally do not impart a narrow requirement for a specific environment, but rather a unique set of "ranges of tolerance" to a large array of environmental parameters. In different environmental contexts, different tolerances may be more limiting, both abiotic and biotic interactions may be altered, and the same set of species may sort out in different spacial patterns. A further consequence of this is that a local combination of species, which we might refer to as a Great Basin plant community, represents a region of overlap in the geographically more extensive and generally unique distributions of each component species. In fact, the distributions of species commonly associated in the same Great Basin community may be strongly contrasting outside the Great Basin. This is an essential point in attempting to discuss plant adaptations with the implication of cause and effect, because few species discussed will have a strict and exclusive relationship with the environment of interest. Unless we can show local, ecotypic differentiation in the traits discussed, we need to take a broad view of the relationship between environment and plant characters. In a few instances, a small number of edaphic factors and plant characters, such as tolerance of very high salinity in soil with shallow groundwater, seem to be of overriding importance. In most cases we need to ask, what are the common elements of climate over the diverse ranges of all these species? One such common element, which will be emphasized throughout this review, is the importance of reliable winter recharge of soil moisture in an arid to semiarid climate. By identifying such common elements and focusing on them, we do not fully describe the autecology of any species, but we attempt a cogent treatment of plant adaptations to the Great Basin environment, and an explanation of the unique features of its plant communities.

CLIMATE, EDAPHIC FACTORS, AND PLANT DISTRIBUTION PATTERNS

Typical zonation patterns observed in species distributions around playas (the saline flats at the bottom of closed-drainage basins) are quite dramatic, reflecting an overriding effect of salinity on plant distribution in the Great Basin. Moving out from the basin center is a gradient of decreasing soil salinity often correlated with progressively coarser-textured soils. Along this gradient there are conspicuous species replacements, often resulting in concentric zones of contrasting vegetation (Flowers 1934, Vest 1962). In the lowest topographic zone, saline groundwater may be very near the surface. Soils are very saline, fine textured, and subject to occasional flooding and anoxic conditions. In this environment the combination of available moisture with other potentially stressful soil characteristics seems to be more important than climatic factors of temperature or seasonal rainfall patterns. Species found here, such as desert saltgrass (*Distichlis spicata*), pickleweeds (*Allenrolfia occidentalis* and *Salicornia* spp.), and greasewood (*Sarcobatus vermiculatus*), may themselves show zonation due to degrees of tolerance. They tend to occur in close proximity, however, on the edges of salt playas, saline flats with shallow water tables, and near saline seeps over a wide range of elevations, temperatures, and seasonal rainfall patterns in both the Great Basin and southern warm deserts (MacMahon 1988). This relative independence of distribution from prevailing climate is a special characteristic of strongly halophytic plant communities throughout the world and reflects the overriding importance of such extreme edaphic conditions. Species found on better-drained, moderately saline soils, where groundwater is not found within the rooting zone, include winterfat (*Ceratoides lanata*) and shadscale (*Atriplex confertifolia*). These species are, in turn, replaced at higher elevations and on moister, nonsaline soils by big sagebrush (*Artemisia tridentata*), rabbitbrush (*Chrysothamnus* sp.), bitterbrush (*Purshia* sp.), and spiny hopsage (*Grayia spinosa*). Shadscale is often found in areas where soils are notably saline in the lower half of the rooting zone, but not in the upper soil layers. Such a tolerance of moderately saline soils seems to control its distribution around playas, especially in the wetter, eastern portion of the Great Basin (western Utah) and lower elevations in the warm Mojave Desert. In the more arid regions of western and central Nevada, however, the shadscale community occurs widely on nonsaline slopes lower in elevation, warmer, and drier than those dominated by big sagebrush. These higher bands of shadscale have been variously interpreted in terms of aridity tolerance and climate (Billings 1949) or an association with limestone-derived calcareous soils (Beatley 1975). The latter author points out that even on nonsaline soils percent cover in the shadscale community is lower than expected for the level of precipitation, and argues that this indicates stress from edaphic factors. Thus, shadscale distribution is most correlated with salinity tolerance in some regions and other edaphic and climatic tolerances in other regions.

Where the higher elevations of the Great Basin come in contact with the lower-elevation, generally drier, and warmer Mojave Desert region, communities dominated by creosote (*Larrea tridentata*) replace sagebrush communities on nonsaline slopes and bajadas.

Shadscale can be found both on saline soils at very low elevations in the Mojave and as a transitional band at high elevations between creosote and sagebrush. Elements of the cold desert shrub communities, adapted to continental winters and a cool spring growing season, can be found throughout the winter-rain-dominated Mojave Desert region as a high-elevation band on arid mountain ranges. They also extend to the southeast at high elevations into the strongly bimodal precipitation regime of the Colorado Plateau, and northward at low elevations into Idaho, Washington, and even British Columbia. Moving up from bajadas of the southern warm deserts, there appears to be no suitable combination of temperature and precipitation at any elevation to support floristic elements of the cold desert. As precipitation increases with altitude, zones with equivalent total precipitation do not yet have cold winters and are occupied by warm desert shrub communities grading into chaparral composed of unrelated taxa. Higher elevations with cold winters have sufficient precipitation to support forests. Other elements common in shadscale and mixed-shrub communities of the Great Basin, such as winterfat and budsage (*Artemisia spinosa*), are often found outside the Great Basin in cold-winter but largely summer-rainfall grasslands.

From these patterns of community distribution within the Great Basin and Colorado Plateau, and also from a consideration of the more extensive ranges and affinities of the component species, we can isolate a few key features of the environment that are largely responsible for the unique plant features seen in the Great Basin. The most obvious features are related to the patterns of soil salinity and texture generated by the overall aridity combined with either internal drainage basins or the in situ weathering of specific rock types. The most important climatic variables are slightly more subtle. There is clearly not a requirement for exclusively winter rainfall, but there is a requirement for at least a substantial portion of the annual rainfall to come during a continental winter. This permits winter *accumulation* of precipitation to a *greater depth* in the soil profile than will occur in response to less predictable summer replenishment of drying soil moisture reserves. Under an overall arid climate, winter recharge maintains a predictably favorable and dominant spring growing season even in many areas of strongly bimodal rainfall. Most of the physiological, morphological, and phenological traits found in the dominant shrubs reflect the primary importance of such a cool spring growing season.

PHOTOSYNTHESIS

PHOTOSYNTHETIC PATHWAYS.—The process of photosynthesis in plants relies on the acquisition of CO_2 from the atmosphere, which, when coupled with solar energy, is transformed into organic molecules to make sugars and provide for plant growth. In moist climates plant communities often achieve closed canopies and 100% cover of the ground surface. Under these conditions competition for light may be among the most important plant-plant interactions. In the deserts total plant cover is much less than 100%, and in the Great Basin closer to 25%. Photosynthesis is not greatly limited by available light, but rather by water, mineral nutrients needed to synthesize enzymes and maintain metabolism, and maximum canopy leaf-area development.

Three biochemical pathways of photosynthesis have been described in plants that differ in the first chemical reactions associated with the capture of CO_2 from the atmosphere. The most common and most fundamental of these pathways is referred to as the C_3 pathway because the first product of photosynthesis is a 3-carbon molecule. The other two pathways, C_4 and CAM, are basically modifications of the primary C_3 pathway (Osmond et al. 1982). The C_4 pathway (first product is a 4-carbon molecule) is a morphological and biochemical arrangement that overcomes photorespiration, a process that results in reduced photosynthetic rates in C_3 plants. The C_4 pathway can confer a much higher temperature optimum for photosynthesis and a greater water-use efficiency. As water-use efficiency is the ratio of photosynthetic carbon gain to transpirational water loss, C_4 plants have a metabolic advantage in hot, dry environments when soil moisture is available. In grasslands C_4 grasses become dominant at low elevations and low latitudes where annual temperatures are warmest. In interpreting plant distribution in deserts, the seasonal pattern of rainfall usually restricts the periods of plant growth, and the temperature during the rainy season is thus more important than mean annual temperature. The C_4 pathway is often associated with summer-active species and also with plants of saline soils. While C_3 grasses predominate in most of the Great Basin, C_4 grasses become increasingly important as summer rain increases to the south, and especially on the Colorado Plateau. Halophytic plants are often C_4, such as saltbush (*Atriplex* spp.) and saltgrass (*Distichlis* spp.), and this may give the plants a competitive advantage from increased water-use efficiency on saline soils.

The third photosynthetic pathway is CAM photosynthesis (Crassulacean Acid Metabolism). CAM plants open their stomata at night, capture CO_2 and store it as malate in the cell vacuole, and keep their stomata closed during the day (Osmond et al. 1982). The CO_2 is then released from the vacuole and used for photosynthesis the following day. Because the stomata are open only at night when it is cool, water loss associated with CAM photosynthesis is greatly reduced. This pathway is often found in succulents such as cacti and agave, and, although CAM plants are present in the Great Basin, they are a relatively minor component of the vegetation.

Photosynthetic rates of plants, like most metabolic processes, show a strong temperature dependence. Usually, photosynthetic rates are reduced at low temperatures because of the temperature dependence of enzyme-catalyzed reaction rates, increase with temperature until some maximum value (which defines the "temperature optimum"), and then decrease again at higher temperatures. The temperature optima and maximum photosynthetic rates of plants show considerable variation, and they generally reflect the growing conditions of their natural environments.

PHOTOSYNTHETIC ADAPTATION.—In the spring the photosynthetic temperature optima of the dominant shrub species are typically as low as 15 C (40 F) (Caldwell 1985), corresponding to the prevailing environmental temperatures (midday maxima generally less than 20 C). As ambient temperatures rise 10–15 C in the summer, there is an upward shift of only 5–10 C in the photosynthetic temperature optima of most shrubs, coupled with a slower decline of photosynthesis at high temperatures. The maximum photosynthetic rates measured in most Great Basin shrubs under either natural or irrigated conditions range from 14 to 19 μmol CO_2 m^{-2} s^{-1} (DePuit and Caldwell 1975, Caldwell et al. 1977, Evans 1990). These rates are quite modest compared to the high maxima of 25 to 45 μmol CO_2 m^{-2} s^{-1} observed in many warm-desert species adapted to rapid growth at higher temperatures (Ehleringer and Björkman 1978, Mooney et al. 1978, Comstock and Ehleringer 1984, 1988, Ehleringer 1985). This presumably reflects the specialization of these Great Basin shrubs towards utilization of the cool spring growing season. Positive photosynthetic rates are maintained even when leaf temperatures are near freezing, which permits photosynthetic activity to begin in the very early spring (DePuit and Caldwell 1973, Caldwell 1985).

Unusually high maximum photosynthetic rates of 46 μmol CO_2 m^{-2} s^{-1} have been reported for one irrigated Great Basin shrub, rabbitbrush (*Chrysothamnus nauseosus*) (Davis et al. 1985). This species is also unusual in having a deep tap root that often taps groundwater, unusually high levels of summer leaf retention (Branson et al. 1976), and continued photosynthetic activity throughout the summer drought (Donovan and Ehleringer 1991). All of these characters suggest greater photosynthetic activity during the warm summer months than is found in most Great Basin shrub species.

SHOOT ACTIVITY AND PHENOLOGY.—Generally speaking, there is a distinct drought in early summer (June–July) in the Great Basin Cold Desert, the Mojave Desert, and the Sonoran Desert. All of these deserts have a substantial winter precipitation season, but they differ in the importance of the summer and early fall rainy season (July–October) in supporting a distinctive period of plant growth and activity (MacMahon 1988). The relationship between climate and plant growing season is complex and includes total rainfall, seasonal distribution of rainfall, and predictability of rainfall in different seasons as important variables. Furthermore, in very arid areas the seasonality of temperatures may be as important as that of rainfall. In the Great Basin, cold winters allow the moisture from low levels of precipitation to accumulate in the soil for spring use, while hot summer temperatures cause rapid evaporation from plants and soil. High temperatures can prevent wetting of the soil profile beyond a few centimeters depth in response to summer rain, even when summer rain accounts for a large fraction of the annual total (Caldwell et al. 1977). As total annual rainfall decreases, the relative importance of the cool spring growing season increases as the only potential growing period in which available soil moisture approaches the evaporative demand (Thornthwaite 1948, Comstock and Ehleringer 1992). Finally, reliability of moisture is important to perennials, and as average total precipitation decreases, the variance between years increases (Ehleringer 1985); variability of annual precipitation is discussed in more detail later in the section on annuals and life-history diversity. Summer rain is more likely to be concentrated in a few high-intensity storms that may not happen every year at a given site and may cause more runoff when they do occur. The ability of moisture from winter rain to accumulate over several months greatly enhances its reliability as a moisture resource. Thus, most plants in the Great Basin have their primary growing season in the spring and early summer. Some species achieve an evergreen canopy by rooting deeply, but few species occur that specialize on growth in the hot summer season (Branson et al. 1976, Caldwell et al. 1977, Everett et al. 1980). Ehleringer et al. (1991) measured the ability of common perennial species in the Colorado Plateau to use moisture from summer convection storms. They observed that less than half of the water uptake by woody perennial species was from surface soil layers saturated by summer rains. Prevalence of summer-active species increases along the border between higher basins and the southeast Mojave Desert where summer rain is more extensive, and especially on the Colorado Plateau where summer rain is greatest. Summer temperatures are also lower on the Colorado Plateau than in the eastern Mojave (Table 1), allowing more effective use of the moisture.

Most phenology studies, especially from the more northern areas, emphasize the directional, sequential nature of the phenological phases (Branson et al. 1976, Sauer and Uresk 1976, Cambell and Harris 1977, West and Gastro 1978, Pitt and Wikeem 1990). A single period of spring vegetative growth is usually followed by a single period of flowering and reproductive growth. Many species produce a distinct cohort of ephemeral spring leaves and a later cohort of evergreen leaves (Daubenmire 1975, Miller and Schultz 1987). For most species, multiple growth episodes associated with intermittent spring and summer rainfall events do not occur. In years with unusually heavy August and September rains, a distinct second period of vegetative growth may occur in some species (West and Gastro 1978). Climatic variations from year to year do not change the primary importance of spring growth or the order of phenological events. In particular years, they may cause expansion or contraction of vegetative phases and even the omission of reproductive phases.

Most species initiate growth in early spring (March) when maximum daytime temperatures are 5–15 C and while nighttime temperatures are still freezing. Delayed initiation of spring growth is generally associated with greater summer activity and may be related to an evergreen habit, a phreatophytic habit, or occupation of habitats with greater summer moisture availability from regional rainfall patterns, runoff, or groundwater. Higher-than-average winter and spring precipitation tends to prolong vegetative growth and delay reproductive growth till later in the summer (Sauer and Uresk 1976, Cambell and Harris 1977). Strong vegetative dormancy may be displayed in mid-summer (Everett et al. 1980, Evans 1990), although root growth (Hodgkinson et al. 1978) and increased reproduction (West and Gastro 1978, Evans, Black, and Link 1991) may still occur in response to rain at that time. In years with below-average spring and summer precipitation, leaf senescence is accelerated and flowering may not occur in many species.

The time taken to complete the full annual growth cycle including both vegetative and reproductive stages is strongly related to rooting depth in most of these communities, with deep-rooted species prolonging activity further into the summer drought (Pitt and Wikeem 1990). The exact timing of flowering and fruit set shows considerable variation among different shrub species. Some, especially those that are drought-deciduous, flower in late spring and early summer just prior to or concurrent with the onset of summer drought. Many evergreen shrub species begin flowering in midsummer (*Artemisia*) or in the fall (*Gutierrezia* and *Chrysothamnus*). These late-flowering species generally do not appear to utilize stored reserves for flowering, but rely on current photosynthesis during this least favorable period. In the case of *Artemisia tridentata*, it has been shown that carbohydrates used to fill fruits are derived exclusively from the inflorescences themselves, while photosynthate from vegetative branches presumably continues to support root growth. Summer rain during this time period does not promote vegetative shoot growth but does increase water use by and the ultimate size of inflorescences (Evans 1990). Evans, Black, and Link (1991) have argued that this pattern of flowering, based on residual deep soil moisture and the unreliable summer rains, may contribute to competitive dominance within these communities. The more favorable and much more reliable spring growing season is used for vegetative growth and competitive exploitation of the soil volume, while reproductive growth is delayed until the less favorable season, and may be successful only in years with adequate summer precipitation.

Most grasses in the northern part of the Great Basin utilize the C_3 pathway and begin growth very early in the spring. These species complete fruit maturation by early or midsummer, often becoming at least partially dormant thereafter. On the Colorado Plateau, with much greater amounts of summer precipitation, there is a large increase in species number and cover by C_4 grasses such as bluestem (*Andropogon*) and grama (*Bouteloua*), especially at warmer, lower elevations and on deep sandy soils. Many of these species occur in mixed stands with the C_3 species but delay initiation of growth until May or June; they can be considered summer-active rather than spring-active. In contrast, some C_4 grasses such as sand dropseed (*Sporobolus cryptandrus*), galleta grass (*Hilaria jamesiii*), and three-awn (*Aristida purpurea*) are widespread in the Great Basin where summer rain is only moderate in long-term averages and very inconsistent year to year. Spring growth of these widespread species tends to be slightly or moderately delayed compared to co-occurring C_3 grasses, but they are still able to complete all phenological stages based on the spring moisture recharge. They show a greater ability than the C_3 species to respond to late spring and summer rain with renewed growth (Everett et al. 1980), however, which compensates in some years for their later development. Other C_4 grasses in the Great Basin may be associated with seeps, streamsides, or salt-marshes, and show a summer activity pattern. C_4 shrubs such as saltbush (*Atriplex*) show similar, spring-active growth patterns to the C_3 shrubs, but may show slightly greater tolerance of summer drought (Caldwell et al. 1977).

Phenology in the Mojave Desert shows both similarities and strong contrasts to the Great Basin. Although rainfall is largely bimodal in the eastern Mojave, absolute amounts are very low. The summer is so hot that little growth normally occurs at that time unless more than 25 mm (1 inch) comes in a single storm (Ackerman et al. 1980). Fall and winter precipitation is the most important in promoting good spring growth of perennials (Beatley 1974). Comstock et al. (1988), looking at one year's growth in 19 Mojave species, described an important cohort of twigs initiated during the winter period that accounted for most vegetative growth during the following spring. Although new leaves were produced in response to summer rain, summer growth in many of the species was largely a further ramification of spring-initiated floral branches. In most species summer growth made little contribution to perennial stems. Despite the preferred winter-spring orientation of many shrubs, winter recharge is much less effective and reliable in the Mojave Desert than in the Great Basin. Due to warmer temperatures, winter dormancy may be less complete, but vigorous growth rarely occurs until temperatures rise further in the early spring. Rapid growth may be triggered by rising spring temperatures or may be delayed until major spring rains provide sufficient moisture (Beatley 1974, Ackerman et al. 1980). Furthermore, a shallower soil moisture recharge often results in fluctuating plant water status and multiple episodes of growth and flowering during the spring and early fall. Some Great Basin species that also occur in the Mojave, such as winterfat and shadscale, commonly show multiple growth and reproductive episodes per year under that climate (Ackerman et al. 1980) but not in the Great Basin (West and Gastro 1978). The degree to which this difference is due entirely to environmental differences as opposed to ecotypic differentiation does not appear to have been studied.

WATER RELATIONS

ADAPTATION TO LIMITED WATER.—Stomatal pores provide the pathway by which atmospheric CO_2 diffuses into the leaf replacing the CO_2 incorporated into sugar molecules during photosynthesis. Because water vapor is present at very high concentrations inside the leaf, opening stomata to capture CO_2 inevitably results in transpirational water loss from the plant; thus, leaf water content is decreased, resulting in a decrease in plant water potential (Ψ). Thus, plant water status, transpiration, and acquisition of water from the soils have a tremendous impact on photosynthetic rates and overall plant growth.

Many soils in the Great Basin are fine textured, which has both advantages and disadvantages for plant growth. Infiltration of water is slower in fine-textured soils, increasing the likelihood of runoff and reduced spring recharge, especially on steeper slopes. They are also more prone to water-logging and anoxic conditions. The deep root systems of Great Basin shrubs are very sensitive to anoxia, and this can be a strong determining factor in species distributions (Lunt et al. 1973, Groeneveld and Crowley 1988). Unusually wet years may even cause root dieback, especially at depth. Once water enters the soil profile, the extremely high surface areas of fine-textured soils with high clay and silt content give them a much higher water-holding capacity than that found in sandy, coarse-textured soils. Much of this water is tightly bound to the enormous surface area of the small particles, however, and is released only at very negative matric potentials. Plants must be able to tolerate low tissue water potentials to make use of it.

As soil water is depleted during summer, plants reduce water consumption by closing stomata (DePuit and Caldwell 1975, Cambell and Harris 1977, Caldwell 1985, Miller 1988) and reducing total canopy leaf area to a minimum (Branson et al. 1976). Evergreen species shed only a portion of the total canopy, however, maintaining the youngest leaf cohorts throughout the drought (Miller and Schulz 1987). Although physiological activity is greatly reduced by water stress, evergreens such as sagebrush can still have positive photosynthetic rates at leaf water potentials as low as −50 bars (Evans 1990) and may survive even greater levels of stress. In contrast, crop plants can rarely survive prolonged Ψ of less than −15 bars. Remaining functional at low water potentials requires the concentration of solutes in the cell sap, and this appears to be accomplished by several mechanisms. In many mesic species, increases in organic solutes may account for most of the change in osmotic potential. In other species, and especially those that experience very low leaf water potentials, a large fraction of the solutes is acquired by the uptake of inorganic ions such as $K+$ (Wyn Jones and Gorham 1986). High concentrations of inorganic ions may be toxic to enzyme metabolism, however, and they are widely thought to be sequestered largely in the central vacuole, which accounts for 90% of the total cell volume, even though much of the evidence for this is quite indirect. Nonetheless, the osmotic potential of the cytoplasm must also be balanced or suffer dehydration. The cytoplasmic solutes must have the special property of lowering the osmotic potential of the cell sap without disrupting enzyme function or cellular metabolism, and are hence termed "compatible" solutes (Wyn Jones and Gorham 1986). The use of specific molecules shows considerable variation across species apparently due to both species-specific variations in cell metabolism and taxonomic relationships. Some frequently encountered molecules thought to function in this manner include amino acids such as proline and also special sugar-alcohols. Some plants appear to generate low osmotic potentials by actively manufacturing larger quantities of dissolved organic molecules per cell in response to water stress, a process referred to as "osmotic adjustment." This process may be costly, however, requiring the investment of large amounts of materials (new solutes) at a time when water stress is largely inhibiting photosynthetic activity. An alternative method seems to involve dramatic changes in cell water volume. Several desert species have been observed to reduce cell water volume by as much as 80% without wilting when subjected to extremely low soil water potentials (Moore et al. 1972, Meinzer et al. 1988, Evans et al. 1991). This allowed the leaf cells to have sufficiently low osmotic potentials for water uptake even though solute content per cell was actually reduced. Although total solutes per leaf (and presumably per cell) decreased, the relative concentrations of specific solutes changed (Evans et al. 1991) such that "compatible" solutes made larger contributions to the osmotic potential under stress. Thus, tolerance of low leaf water potentials was achieved by a combination of anatomical and physiological specializations. The anatomical mechanisms involved in this magnitude of volume reduction and the implied cell elasticity have not been studied, but the process has been shown to be fully reversible.

Soil texture is also an important factor in determining the ability of plant communities in a cold-winter climate to respond to summer rain. In areas with moderate levels of precipitation, sandy soils, because of their low water-holding capacity, usually hold a sparser, more drought-adapted vegetation than finer-textured ones. In warm, arid areas, however, what has been called the "reverse texture" effect results in the more lush vegetation occurring in the coarse-textured soils. This occurs because the high water-holding capacity of fine-textured soils allows them to hold all the moisture derived from a single rainfall event in the uppermost layers of the soil profile, where it is highly subject to direct evaporation from the soil. The same amount of rainfall entering a sandy soil, precisely because of its low water-holding capacity, will penetrate to a much greater depth. It is also less likely to return to the drying surface by capillary action. Less of the rain will evaporate from the soil surface, and a greater fraction of it will await extraction and use by plants. This inverse-texture effect further restricts the effectiveness of summer rains in the fine soils of the Great Basin. The effect is less operative in respect to winter precipitation in the Great Basin, however, because of the gradual recharge of the soil profile to considerable depth under conditions where surface evaporation is minimized by cold temperatures. The combination of much sandier soils and greater amounts of summer rainfall in the region of the Colorado Plateau is largely responsible for the major floristic and ecological differences between the two regions. At lower elevations on the southeast edge of the plateau, shrub-dominated desert scrub may be replaced by grassland dominated by a mix of spring-active C_3 and summer-active C_4 species.

ROOTING DEPTH, MORPHOLOGY, AND PHENOLOGY.—One of the unique and ecologically most important features of the Great Basin shrub communities is not apparent to aboveground observers. This is the investment of the vast majority of plant resources in the growth, maintenance, and turnover of an enormous root system. The dominant shrubs of the Great Basin usually root to the full depth of the winter-spring soil moisture recharge. Depending on soil texture, slope aspect, and elevation, this is generally between 1.0 and 3.0 m (Dobrowolski et al. 1990). Although this represents a wide range of absolute depths, many of the qualitative patterns of rooting behavior are similar on most of these sites. Ratios of root:shoot standing biomass range from 4 to 7, and estimates of root:shoot annual carbon investment are as high as 3.5. Most of the shrubs have a flexible, generalized root system with development of both deep taproots and laterals near the surface. Moreover, it is the category of fine roots < 3.0 mm in diameter that constitutes 50–95% (Caldwell et al. 1977, Sturges 1977) of the total root biomass. The very large annual root investments, therefore, are not primarily related to large storage compartments, but to the turnover of fine roots and root respiration necessary for the acquisition of water and mineral nutrients.

The fine root network thoroughly permeates the soil volume. Root densities are generally quite high throughout the upper 0.5 meters of the profile, but depth of maximum root development varies with depth of spring soil-moisture recharge, species, and lateral distance from the trunk or crown. A particularly high density in the first 0.1 m may often occur, especially immediately under the shrub canopy (Branson 1976, Caldwell et al. 1977, Dobrowolski et al. 1990). Alternatively, maximal density may occur at depths between 0.2 m and 0.5 m (Sturges 1980), and sometimes a second zone of high root density is reported at depths of 0.8 m (Daubenmire 1975) to 1.5 m (Reynolds and Fraley 1989). Regardless of the precise depth of maximum rooting, shrub root density is usually high throughout the upper 0.5 m and then tapers off, but may continue at reduced densities to much greater depth. The radius of lateral spread is usually much greater for roots (1–2 m) than for canopies (0.1–0.5 m). Percent plant cover aboveground is often in the neighborhood of 25% with 75% bare ground, but belowground the interspaces are filled with roots throughout the profile, and root systems of adjacent plants will overlap. The perennial grasses that are potentially co-dominant with shrubs in many of these communities, such as wheatgrass (*Agropyron* sp.), wildrye (*Elymus* sp.), squirreltail (*Sitanion histrix*), Indian ricegrass (*Oryzopsis hymenoides*), and galleta grass (*Hilaria jamesii*), generally have somewhat shallower root systems than the shrubs (Branson et al. 1976, Reynolds and Fraley 1989, Dobrowolski et al. 1990). Root densities of grasses are often as high as or higher than those of shrubs in the upper 0.5 m but taper off more rapidly such that shrubs usually have greater density at depth and greater maximum penetration.

The moisture resource supporting the greatest amount of plant growth is usually the water stored in the soil profile during the winter. This profile usually has a positive balance, with more water being added by precipitation than is withdrawn by evapotranspiration between October and March. As temperatures warm in March, evergreen species may begin drawing on this moisture reserve, and most species begin active growth in March or April. Due to both plant water use and soil-surface evaporation, soil moisture is depleted first in the shallow soil layers. As the upper layers dry, plants withdraw moisture from successively deeper soil layers, a process that continues in evergreen species throughout the summer until soil moisture is depleted throughout the profile. This progression of seasonal water use beginning in superficial layers and proceeding to deeper soil layers is facilitated by the pattern of fine root growth, which shows a similar spatial and temporal pattern (Fernandez and Caldwell 1975, Caldwell 1976). Root growth generally precedes shoot growth in the early spring and continues throughout the summer in evergreen species, which may appear quiescent aboveground. In annual budgets of undisturbed communities, soil moisture withdrawal almost always approaches measured precipitation over a wide range of annual fluctuations in total precipitation, and very little moisture is lost to runoff or deep drainage beneath the rooting zone (Daubenmire 1975, Caldwell et al. 1977, Cambell and Harris 1977, Sturges 1977). Calculations of the portion of evapotranspiration actually used by plants in transpiration are quite high for a desert environment with low percent cover; they range from 50 to 75% (Caldwell et al. 1977, Cambell and Harris 1977, Sturges 1977).

Competition for soil moisture is not necessarily limited to any single season. Plant water stress is highest in late summer, and survival is most likely to be influenced at this time, especially if one plant can deplete residual soil moisture below the tolerance range of another. This has been shown in several cases with regard to seedling establishment (Harris 1977, DeLucia and Schlesinger 1990, Reichenberger and Pyke 1990). Growth and productivity are more likely to be affected in the spring and early summer growing season. This is because most of the year's water resource is already stored in the soil in early spring, and all plants are drawing on a dwindling reserve which ultimately determines growing season length. Competitive ability is often found to be associated with an ability to begin using the limiting water resource earlier in the spring (Eissenstat and Caldwell 1988, Miller 1988), but spatial partitioning is also important. Competition may be most intense in shallower soil layers because grasses and drought-deciduous shrubs, which are active only in the spring, are shallower rooted, and lateral root spread of the evergreen species is greatest in the shallower soil layers. The more dominant perennials usually use more water over the whole season by tapping deeper soil layers (Cline et al. 1977, Sturges 1980) and are characterized by higher water-use efficiencies (DeLucia and Schlesinger 1990, Smedley et al. 1991).

Shrubs appear to be better than grasses at withdrawing water from deep soil layers for several reasons. In shallow soils underlain by fractured or porous bedrock, the flexible, multiple taproot structure of a shrub root system may be better suited than the more diffuse, fibrous root system of grasses for following chinks and cleavage planes to indeterminate depths. This should allow shrubs to better capitalize on deep, localized pockets of moisture. Unfortunately, such dynamics are rarely studied quantitatively because of the difficulty of measuring soil moisture budgets or root distributions under such conditions, but they are implicated by plant distribution patterns in many areas. Indeed, despite the visual austerity of such habitats, rooting into major joints and cracks in bedrock outcrops can create such a favorable microsite by concentration of runoff in localized areas that elevational limits of tree and shrub distributions may be substantially lowered as would be expected along riparian corridors or other unusually mesic habitats (Loope 1977). Even in deep soils, shrubs tend to have deeper root systems than grasses, but, in addition to this, shrubs may be more efficient than grasses at extracting deep water. Shrubs are sometimes able to draw on deep soil moisture to a greater extent than would be predicted from root biomass distribution alone (Sturges 1980), and this is due in part to an intriguing phenomenon reported by Richards and Caldwell (1987), and named by them "hydraulic lift." During the late spring and early summer most of the remaining soil moisture is present in deeper soil layers where rooting density may be relatively low. Due to low densities, deep roots alone may be unable to absorb water as quickly as it is lost by the transpiring shoot. During the night, water is actually redistributed within the soil, flowing from deep soil layers through the roots and back out into shallower soil layers. This is the phenomenon named "hydraulic lift," and the advantage to the plant is thought to be a reduction in the rooting density necessary to fully exploit the resources of the deepest soil layers. During the day, rates of water movement from the soil into the roots can be limiting to shoot activity. Moistening the upper soil layers by nocturnal hydraulic lift increases the root surface area for absorption during the periods of high transpiration. Daytime water use can be supported by the entire root system and not just by the low-density deep roots (Caldwell and Richards 1989).

The root systems of Great Basin shrubs and Mojave Desert shrubs differ strongly in several ways. (1) Mojave Desert shrubs often have maximal rooting densities at soil depths of 0.1–0.3 m, and maximum root penetration of 0.4–0.5 m (Wallace et al. 1980). These shallower roots are due to lower rainfall and warmer winter temperatures resulting in shallower wetting fronts in the soil, and the development of shallow caliche layers. (2) Great Basin species have more roots in the shallowest 0.1 m soil layer (Wallace et al. 1980, Dobrowolski et al. 1990). Differences in soil temperatures have been used to explain these patterns, but the link between cause and effect is less obvious in this case, and conjectures should be viewed cautiously. Much hotter soil temperatures in the Mojave may be detrimental to roots in the uppermost few centimeters during summer, and the rapidly drying soil surface may be too ephemeral a moisture resource to favor large investments in roots. In contrast, snowmelt and cooler spring temperatures may result in less rapid evaporation from the soil surface in the Great Basin and thus favor more rooting by perennials in that zone. (3) Because of the greater soil volume exploited, as well as the high root density of Great Basin species, their ratios of root:shoot biomass are about twice that of Mojave Desert species (Bamberg et al. 1980, Dobrowolski et al. 1990).

ADAPTATION TO SALINITY.—When annual precipitation levels are much lower than potential evaporation, salts are not leached to any great depth, and they can accumulate within the root zone. This is especially important in association with particular bedrock outcrops, such as the Mancos and Chinle shales, which release high concentrations of salts during weathering (Potter et al. 1985). Precipitation increases with elevation, and, following major storms or spring snowmelt, there may be surface runoff and recharge of groundwater systems that transport water from high elevations into closed basins. Streams in the Great Basin usually terminate in evaporative pans where salinities reach extreme levels and salts precipitate forming a surface crust. The water table near these evaporative pans is often at or very near the surface throughout the year, but, if there is no groundwater flow out of the basin, it too is often quite saline (Dobrowolski et al. 1990). Salinities are lowest on slopes and at higher elevations where precipitation exceeds evaporative loss, and they increase on more level terrain and in lower-elevation basins where evaporation exceeds precipitation. Salinities may also be higher in areas where wind-borne materials are transported from saline playas to surrounding slopes (Young and Evans 1986). These patterns of soil salinity are important in determining plant distributions, with more specialized salt-tolerant species (halophytes) replacing less-tolerant species repeatedly along gradients of increasing salinity. In general, species diversity is low on saline soils. The vast majority of tolerant shrub species in our deserts, and all the shrubs specifically mentioned in this section, belong to a single plant family, the Chenopodiaceae (goosefoot family). Most other important taxa in the saline communities are grasses.

In the most extreme case of hypersaline salt flats and pans there may be standing water in the wet season with saturating salt concentrations. Under such conditions, only microflora consisting of a few species of photosynthetic flagellates, cyanobacteria, and halobacteria are commonly found. The halobacteria appear to be unique in having adapted in an obligate manner to the high salinities of these environments. They not only tolerate, but *require*, high cytoplasmic salinities for membrane stability and proper enzymatic function (Brown 1982). In strong contrast to this, algae and all higher plants growing in hyper-saline environments show severe inhibition of enzyme function at high salinity, and they must compartmentalize salt-sensitive metabolic processes in cellular regions of low ionic strength (Munns et al. 1982).

The best definition of a halophyte is simply a plant tolerant of soil salinities that would reduce the growth of unspecialized species. This is somewhat circular, and that reflects our limited understanding of how halophytes do what they do. Halophytes are more likely to use Na+ in their tissues for osmotic adjustment, while glycophytes are more likely to have high K+ (Hellebust 1976, Flowers et al. 1977), but there are numerous exceptions. Other differences may be more quantitative than qualitative. Various aspects of mineral nutrition in halophytes are less sensitive to high soil salinities, but unique mechanisms to achieve this tolerance have rarely been identified. It is widely held that the ability to compartmentalize salts and restrict high Na+ concentrations to the vacuole is of crucial importance (Caldwell 1974, Flowers et al. 1977, Briens and Larher 1982). This conclusion is based primarily on indirect evidence of low enzyme tolerance of salinity, however, rather than direct measurements of actual salt compartmentalization (Munns et al. 1982, Jefferies and Rudmik 1984).

Halophytes differ in which ions reach high tissue concentrations when all plants are grown on the same medium (Caldwell 1974). Some will concentrate Cl−, for instance, while others concentrate SO_4^{-2}. These differences do not necessarily determine plant distributions, such as occurrence in soils dominated by NaCl versus $NaSO_4$, but rather seem to reflect different regulatory specializations in plant metabolism (Moore et al. 1972). A strong requirement for a unique composition of soil salts is the exception rather than the rule, and the most important effect of soil salinity seems to be a disruption of plant water relations from low soil osmotic potentials rather than toxic effects of specific ions. Halophytes tolerate these conditions by having better regulatory control over ion movement within the plant, ion compartmentalization at both tissue and subcellular levels, and better homeostasis of other aspects of mineral nutrition in the presence of very high Na+.

Salinity poses three major problems for higher plants. First, salts in the soil solution contribute an osmotic potential depressing the soil water potential, and this may be aggravated as salts become concentrated with soil drying. Even when substantial moisture is present, plant tissues must endure very low water potentials to take it up, and this requires a specialized metabolism. Second, any salts entering the plant with the transpiration stream will be left behind in the leaf intercellular fluids as water evaporates from the leaf. This can result in salt buildup in the intercellular solution causing water movement out of the cells and leading to cellular dehydration. Third, salts entering the cytoplasm in high concentration will disrupt enzyme function. Halophytes are able to deal with all of these factors over a wide range of soil salinities. Halophytes show a greater capacity for osmotic adjustment, and positive photosynthetic rates can be measured in the leaves of many halophytes at leaf water potentials as low as −90 to −120 bars (Caldwell 1974), well below the range that would result in death of even desert-adapted glycophytes. This is accomplished in part by transforming the available salts in the environment into a resource and using them for osmotica in plant tissues (Moore et al. 1972, Bennert and Schmidt 1984). Many halophytes actually show stimulation of growth rates at moderate environmental salt levels.

Halophytes too must deal with the problem of salt buildup in the leaves, and they do so by a wide variety of processes. There is a great deal of interspecific variation in which method(s) are used. All the methods appear to incur substantial energetic costs associated with maintaining high ion concentration gradients across key membranes (Kramer 1983). Exclusion of salts at the root is possible; this is the method most employed by winterfat (*Ceratoides lanata*). Saltbush (*Atriplex* spp.) has specialized hair-bladders on the leaf surface into which excess salts are actively pumped. The hairs eventually rupture, excreting the salts to the outside. Other plants may transport salts back to the root via the phloem. Many plants exhibit increased leaf succulence when grown under high salinity, and this increase in cell volume can create a sink for salts within the leaf without raising salt concentrations or further lowering leaf osmotic potential.

In strong contrast to the evident importance of temperature and rainfall pattern in favoring C_3 versus C_4 grasses, C_4 shrubs tend to belong to edaphic communities associated with saline soils. The same species may occur in both warm and cold deserts, and in areas with both winter and summer rainfall patterns. This is an intriguing difference, but the physiological basis linking C_4 shrubs with high salinity is less well understood than the tradeoffs associated with temperature and controlling C_3 and C_4 grass distributions. Species number and percent cover by shrubs such as saltbush (*Atriplex* spp.) and inkweed (*Sueda* spp.), which possess the C_4 pathway, usually increase dramatically with increasing salinity on well-drained soils. In marshy habitats or soils with a shallow, saline water table, however, halophytic C_3 species such as pickleweeds (*Allenrolfia* spp. and *Salicornia* spp.) and greasewood (*Sarcobatus vermiculoides*) regain dominance. It has been suggested that higher water-use efficiency by C_4

species may be advantageous on saline soils to help avoid salt buildup in the leaf tissues. However, it has not been shown that transpiration rate is an important factor controlling salt buildup in the leaves of halophytes when compared with other regulatory mechanisms (Osmond et al. 1982), nor does this hypothesis explain the dominance of C_3 species in wet saline soils. In the greasewood and pickleweed communities, soil salinities are extreme, but soils remain wet throughout the growing season, or else groundwater is available within the rooting zone (Detling 1969, Hesla 1984). As a consequence, plant water potentials do not reach the extreme low values of the saltbush communities. Over a wide range of soil salinities, plants such as greasewood appear to draw on readily available deep soil moisture, and high leaf conductances are maintained throughout the summer (Hesla 1984, Romo and Hafercamp 1989). The highest whole-plant water-use rates may occur in the presence of high soil salinity in mid-summer (Hesla 1984). The communities in which C_4 shrubs are most prevalent have summer stress from both high soil salinity and mid-summer soil water depletion combined. These species reach much lower plant water potentials during summer than either nonsaline communities or wet-saline communities. The role of C_4 photosynthesis in tolerating these conditions remains to be determined, but it could be related to avoiding excessively low leaf water potentials either by (1) retarding soil moisture depletion, which both lowers the soil matrix potential and concentrates soil salts, or (2) avoiding exacerbation of low soil water potentials due to high flux rates and large water potential gradients between the leaf and root. Water movement in the xylem occurs under tension, and anatomical features that avoid cavitation in the xylem at extremely low water potentials usually reduce the hydraulic conductivity of the xylem per unit cross-sectional area (Davis et al. 1990, Sperry and Tyree 1990). Low specific conductivity of the xylem will, in turn, predispose the plant system to large water potential gradients between roots and shoots, causing an even greater depression of leaf water potential. This problem could be ameliorated either by increased cross-sectional area of the xylem by increased allocation to wood growth, or by features such as C_4 photosynthesis that reduce the flux rate of water associated with photosynthetic activity under warm conditions.

NUTRIENT RELATIONS

ACQUISITION OF MINERAL NUTRIENTS.—Apart from the very high elevation montane zones, water appears to be the most limiting resource in the Great Basin and Colorado Plateau communities. Productivity is usually well correlated with yearly fluctuations in precipitation and spring moisture recharge over a wide range of values (Daubenmire 1975, Kindschy 1982), and competitive success has more often been associated with soil water use patterns than nutrient budgets. Nonetheless, addition of mineral fertilizer sometimes does result in modest increases in productivity, and studies have shown strong effects of neighboring plants on nutrient uptake rates (Caldwell et al. 1987). These dynamics have been less studied than have plant water budgets, and broad ecological relationships are just now being worked out in detail. Nutrient acquisition has been shown to be a major factor determining community composition only in very special habitats such as large sand dunes (Bowers 1982) or unusual bedrock (DeLucia and Schlesinger 1990).

MICROPHYTIC CRUSTS.—Throughout the Great Basin and Colorado Plateau, it is common for the exposed soil surface to be covered by a complex community of nonvascular plants including dozens of species of algae, lichens, and mosses (West 1990). These organisms often form a biotic crust in the upper few centimeters of the soil and, when undisturbed, may result in a very convoluted microtopography of the surface. While a detailed discussion of the microphytic crusts is beyond the scope of this review, it is important to realize that percent cover by such crusts often exceeds that of the vascular plants, and their contribution to total ecosystem productivity is considerable. Perhaps most important to co-occurring vascular plants are the nutrient inputs to the soil by nitrogen-fixing crust organisms (cyanobacteria and lichens). These inputs will be particularly important in the cold desert where few vascular plants form symbiotic relationships with nitrogen-fixing bacteria.

NURSE PLANTS AND FERTILE ISLANDS.—In many desert areas, including both the Mojave and the Great Basin, establishment of new individuals may occur preferentially under the existing canopies of already established individuals. These previously established individuals may then be referred to as nurse plants. Preferential establishment under nurse plants may occur in spite of the fact that 75% or more of the ground area may be bare interspaces between plant canopies. The phenomenon can be important in both steady-state community dynamics and also successional patterns following disturbance (Wallace and Romney 1980, Everett and Ward 1984). Two somewhat distinct factors contribute to the nurse-plant phenomenon. The first has to do the with beneficial effects of partial shading and reduced wind under existing canopies resulting in cooler temperatures and possibly moister soil conditions in the surface layers. These interactions depend directly on the presence of the nurse plant in creating a favorable microsite, and have been studied with particular reference to pinyon and juniper establishment in the Great Basin. A second factor involves the creation of fertile islands by the prolonged occupation of the same microsite by many generations of plants; this can make the fertile island a preferred site even if the previous occupant is already deceased. This microsite improvement occurs due to preferential litter accumulation and more extensive root growth directly under a plant canopy, and deposition of aeolian materials under reduced wind speeds in plant canopies. In time, soils under existing plants may come to be slightly raised above the interspace level, have a lighter, loamier texture, higher organic matter content and better soil structure, less surface compaction, better aeration and more rapid water infiltration, and/or higher levels of available mineral nutrients than immediately adjacent interspace soil (Vest 1962, Wood et al. 1978, Romney et al. 1980, Hesla 1984, West 1989, Dobrowolski et al. 1990). Direct effects of nurse plants and indirect effects of fertile islands should complement and reinforce each other in maintaining selective spacial patterns of seedling establishment. Surface soil under halophytes may also show increased salinity (Richard and Cline 1965) due to excretion of excess salts by the canopy or translocation and re-excretion from the roots.

DIVERSITY OF GROWTH FORMS

One of the striking features of the cold desert vegetation is the uniformly low stature of the vegetation. This is undoubtedly due to several factors, and few studies have specifically addressed the role of plant stature in these communities. Since low temperatures may limit photosynthesis in the cool spring, and earlier growth on limited soil moisture reserves may be competitively advantageous, occupying warm microsites may be favored. Substantial increases in air temperature and reductions in wind speed will exist in the lowest meter next to the ground, and especially in the lowest decimeter. Low cushion plants or low, dense shrub canopies should have warmer spring leaf temperatures by virtue of being short and by virtue of leafing out first in a dense clump of old dead leaves and twigs (Smith et al. 1983, Wilson et al. 1987). This advantage may be partially offset by overly high temperatures in summer for species remaining active all summer. Stature is also likely to affect aeolian deposit of materials under the shrub canopies (Wood et al. 1978, Young and Evans 1986), snow accumulation (Branson et al. 1981, West and Caldwell 1983), and the likelihood of winter desiccation under cold, windy conditions (Nelson and Tiernan 1983). All of these could be important factors, but few detailed studies have been done.

Having considered the relationships of the dominant plant habits and phenologies to climate, it is perhaps instructive to consider why some of the other famous desert life forms are so poorly represented in this region. Three life forms which are prominent features of the warm desert but inconspicuous elements of the cold desert are (1) large CAM succulents (e.g., cacti and agave), (2) opportunistic drought-deciduous shrubs specialized for rapid leaf-flushing, and (3) annuals. Definitive work explaining the structural uniformity of the vegetation is not available, but the environment is well enough understood to identify at least some of the likely causes.

CAM SUCCULENTS.—Most of the large CAM succulents are not tolerant of freezing temperatures, and most extant species would be excluded from the Great Basin by this factor alone. There are, however, a sufficient number of species which have adapted to tolerate cold temperatures that we are justified in asking why they have not undergone more adaptive radiation, or claimed a more prominent role in these communities. The most important factor limiting this life form is probably the importance of the cool spring growing season. CAM succulents generally (1) allocate very little biomass to root (root/shoot ca. 0.1), (2) are shallow rooted, (3) store moderate-sized (compared to soil water-holding capacity) water reserves inside their tissues when water is available in the surface soil layers, and (4) use their stored water in photosynthesis with unparalleled water-use efficiency by opening their stomata only at night when temperatures are cool (Nobel 1988). They are favored by (1) very warm days (30–40 C), which allow them to have higher photosynthetic rates and cause competing species to have very low water-use efficiencies; (2) large diurnal temperature fluctuations allowing for cool nights (10–20 C) which allow them to have high rates of CO_2 uptake with high water-use efficiency; and (3) intermittent rainfall, which only wets the upper soil layers so that the limitations of their shallow roots and water-hoarding strategy are compensated for by the ephemeral nature of the soil water resource. These conditions are somewhat poorly met in the cold desert. The important water resource is one of deep soil recharge that favors deep-rooted species and confers much less advantage on internal water hoarding. Freezing tolerance in CAM succulents appears to be associated with low tissue water contents, and this may inhibit uptake of water when it is plentiful in the surface layers in the thermally vacillating early spring (Littlejohn and Williams 1983). Furthermore, water-use efficiencies of C_3 and C_4 species are quite high in the cool spring.

Nonetheless, even moderate amounts of summer rain in the southern and eastern portions of the Great Basin result in numerous species of cacti. Due to the open nature of the understory, many of these species have a large elevational range, and they are often more common in the pinyon-juniper or even the montane zone than on the desert piedmont slopes. Almost all of these cacti are small, usually 5–20 cm high, with a small, globose (e.g., *Pediocactus simpsonii*), prostrate (e.g., *Opuntia polycantha*), or low, caespitose habit (e.g., *Echinocereus triglochidiatus*). This allows them to take advantage of the warmer daytime temperatures near the ground in the spring and facilitates an insulating snowcover during the coldest winter periods. The number of and total cover by cacti increase considerably with increased summer rainfall on the Colorado Plateau, but only in the eastern Mojave with both summer rain and warm spring temperatures do we find the larger barrel-cactus (e.g., *Ferocactus acanthoides*) and tall, shrubby chollas (e.g., *Opuntia acanthocarpa*).

OPPORTUNISTIC DROUGHT-DECIDUOUS / MULTIPLE LEAF-FLUSHING SPECIES.—This habit, like that of the succulents, is favored by (1) intermittent rainfall wetting only shallower soil layers, and (2) warm temperatures allowing for rapid leaf expansion in response to renewed soil moisture. Again, these requirements are not well met in the Great Basin. The primary moisture resource is a single, deep recharge in the winter. Most shrub species are deep rooted, and rather than experiencing vacillating water availability, they have active root growth shifting to deeper and deeper soil layers during the season, thus producing a gradual and continuous change in plant water status. This allows many spring-active shrubs to remain partially evergreen throughout the summer, and, in regions where it occurs, they are able to make rapid use of any moisture available from summer precipitation without the need for renewed leaf production. The only shrub reported to have multiple leaf flushes in response to late spring or summer rain in the Great Basin is the diminutive and shallow-rooted *Artemisia spinescens* (Everett et al. 1980). Some species found in the Great Basin are reported to have multiple growth cycles/year where they occur in the Mojave (Ackerman et al. 1980).

ANNUALS AND LIFE-HISTORY DIVERSITY.—The spectacular wildflower shows displayed in favorable years in the Mojave Desert do not occur in the cold desert of the Great Basin (Ludwig et al. 1988). Annual species are few in number, and, except in early succession after fire in woodlands or on very disturbed sites, they rarely constitute a major fraction of total community biomass. This is undoubtedly related to several complex factors, but various aspects of precipitation patterns are likely to be among the most important. To begin with, the paucity of summer rain in some parts of the Great Basin may largely eliminate an entire class of C_4 summer annuals important in the floras of other regions including the Colorado Plateau. Other aspects than seasonality are also crucial, however. Very low means of annual precipitation are commonly associated with large annual floras, but correlated with low mean precipitation is high year-to-year variation in precipitation which some authors have argued is equally important. The coefficient of variation (CV) in precipitation shows a relationship to mean precipitation in the Great Basin and Colorado Plateau (Fig. 2) very similar to that found in warm

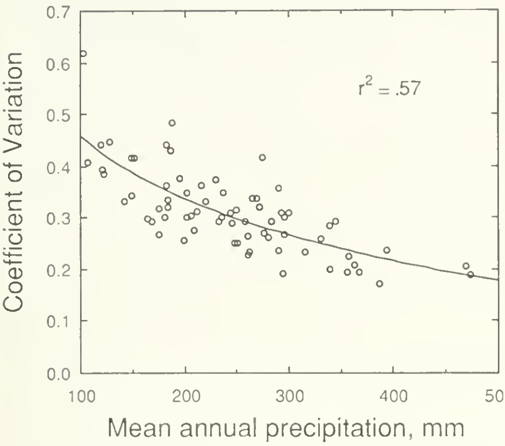

Fig. 2. The relationship between mean precipitation and the variability of rainfall between years as measured by the coefficient of variation in annual precipitation. The data include points scattered throughout the Great Basin in Utah and Nevada and the Colorado Plateau in Utah and Arizona. The line shown is the least squares best fit for the data: CV = 1.27 − 0.403 * log(mean annual precipitation, mm) (n = 69 sites, $p < .001$).

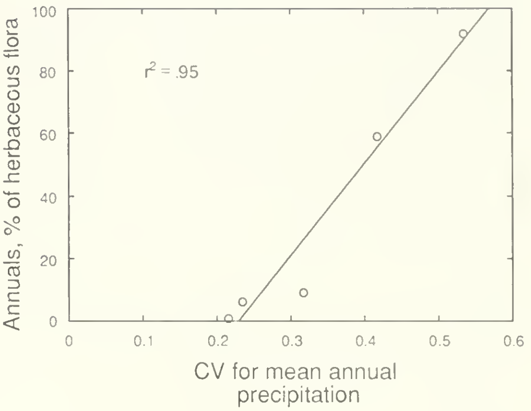

Fig. 3. The relationship between reliability of annual precipitation and life-history strategy of herbaceous plants. The site with greatest representation of annuals is Death Valley in the Mojave Desert, the second highest is Canyonlands in the Colorado Plateau of southeastern Utah, and the other three sites are Great Basin Cold Desert or shrub-steppe (data were collected by Kim Harper and previously published in Schaffer and Gadgil 1975).

deserts (Ehleringer 1985). Although mean precipitation has the greatest single effect, there are, additionally, important geographic influences on the CV of precipitation which are independent of mean precipitation. A multiple regression of the CV of precipitation on log(mean annual precipitation), latitude, and elevation in the Great Basin has an r^2 of .81 and indicates that each variable in the model is highly significant ($p < .001$ or better). For a given mean precipitation, the CV increases with decreasing altitude in the Great Basin, but an independent effect of elevation was not significant in the Colorado Plateau. The CV also increases from north to south in the Great Basin and increases from south to north in the Colorado Plateau, which results in a latitudinal band of greatest annual variability running through southern Nevada and Utah. This band is related to two major aspects of regional climate. Moving southward in the Great Basin, temperatures gradually increase, favoring moister air masses and more intense storms, but sites are more removed from the most common winter storm tracks, and the number of rainy days per year decreases (Houghton 1969). Moving northward from Arizona and New Mexico, the southern Nevada and Utah band of highest precipitation variability also corresponds to the northernmost extent of summer storms associated with the Arizona monsoon, and the region where the fraction of summer rain increases substantially moving southward. This zone also has some of the most arid sites of the entire region located along the transition to the Mojave Desert in southern Nevada and the canyon country of southeastern Utah, and these sites can be expected to have the highest variability due to both low mean rainfall and geographic position correlated with regional weather patterns. Because the Great Basin and Colorado Plateau are only semiarid, the CV of annual precipitation is not usually as high as in many of the more arid warm deserts (Beatley 1975, Ehleringer 1985), but particular sites may be both arid and highly unpredictable.

Harper (cited in Schaffer and Gadgil 1975) found that the prevalence of annuals was positively associated with the CV in annual precipitation for five sites located in the Great Basin, Colorado Plateau, and Mojave Desert (Fig. 3). The largest annual populations occurred in Death Valley (Mojave), followed by Canyonlands (Colorado Plateau in southeastern Utah). One interpretation of this relationship is that high variability in total precipitation between years may be associated with high rates of mortality and therefore favor early reproduction and an annual habit (Schaffer and Gadgil 1975). Many desert annuals are facultatively perennial in better-than-average years, and some have perennial races or sister species (Ehleringer 1985). The dynamics and distributions of these closely related annual and perennial taxa should receive further study in regard to their expected life span, reproductive output, and relationships to climatic predictability. Another perspective is to ask how competition between very distinct shrub and annual species is affected by precipitation variability. While in many respects complementary with the optimal life history arguments, this approach emphasizes how large differences in habit affect resource capture and competition rather than focusing on subtler differences in mortality and reproductive schedules. The lower variability of precipitation in much of the Great Basin compared to the Mojave and Sonoran deserts, as well as the more reliable accumulation of moisture during the winter-recharge season, may favor both stable demographic patterns and growth of perennials. Annuals tend to be shallow rooted (most roots in upper 0.1 m depth), and they are poorly equipped to compete with shrubs for deep soil moisture. If shrub density is high, and years of unusually high mortality are rare, then shrubs may largely preempt the critical water and mineral resources and suppress growth of annuals. The dominant shrubs of the warm deserts do not have high root densities in the upper 10 cm of the soil profile (Wallace et al. 1980), have lower total root densities, and have lower total cover when compared with Great Basin perennials. Annuals are therefore likely to experience more intense competition from shrubs in the Great Basin. This conjecture is further supported by considering that perennials in the Great Basin generally transpire 50% or more of the annual moisture input over a wide range of yearly variations. In the Mojave this fraction may average only 27% and vary between years from 15 to 50% at the same site (Lane et al. 1984), or even be as low as 7% (Sammis and Gay 1979). The reduced overlap in rooting profiles and the greater availability of unused moisture resources may have favored the development of annual floras in the Mojave Desert more than in the Great Basin. With severe disturbance from grazing and other anthropogenic activities, exotic annual species have invaded many Great Basin communities. Once established following disturbance, these annuals are not always easily displaced by short-term shrub succession. While this discussion has been presented in the context of annuals versus perennials, tradeoffs between short- and long-lived perennials may be influenced by very similar climatic parameters, sometimes operating over different time scales.

Other factors that may be important in the ecology of Great Basin annuals include the effects of the very well developed cryptogam soil crusts or vesicular horizons on seed predation (ability of seeds to find safe sites), seed germination, and seedling establishment. The restriction of winter growth by cold temperatures could also be of crucial importance, inhibiting the prolonged establishment period enjoyed by winter annuals in warm deserts. Fall germination followed by low levels of photosynthesis throughout the mild winter is essential for vigorous spring growth of winter annuals in the Mojave, and, while heavy spring rains may cause germination, such late cohorts rarely reach maturity (Beatley 1974). Annuals are common in transition zone sites of the ecotone between Mojave Desert and Great Basin plant communities in southern Nevada, but associated with changes in perennial species composition along decreasing mean temperature gradients in that region are decreases in annual abundance (Beatley 1975).

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LIFE HISTORY, ABUNDANCE, AND DISTRIBUTION OF MOAPA DACE (*MOAPA CORIACEA*)

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ABSTRACT.—Moapa dace (*Moapa coriacea*) is a federally listed endangered fish endemic to the spring-fed headwaters of the Muddy River, Clark County, Nevada. Species life history, abundance, and distribution were studied from March 1984 to January 1989. Reproduction, which was observed year-round, peaked in spring and was lowest in fall. It occurred in headwater tributaries of the Muddy River, within 150 m of warm water spring discharge in water temperatures ranging from 30 to 32 C. Females matured between 41 and 45 mm in fork length (FL). Egg abundance increased with female size (r^2 = .93); counts ranged from 60 for a 45-mm-FL female to 772 for one 90-mm FL. The oldest of eight fish, aged by the opercle method, was a 90-mm-FL, 4+-year-old female. Adults are omnivorous but tended toward carnivory; 75% of matter by volume consumed was invertebrates and 25% plants and detritus. Fish size was generally commensurate with flow, the largest fish occurring in the greatest flow. Adults were near bottom, in focal velocities ranging from 0 to 55 cm/s. Juveniles occupied a narrower range of depths and velocities than adults, and larvae occupied slack water. From December 1984 to September 1987, the total adult population ranged from 2600 to 2800. Although these numbers are higher than previously believed for Moapa dace, they are still sufficiently low to warrant its endangered status. The dependency of Moapa dace's different life history stages to various areas and habitat types of the Warm Springs area suggests that all remaining habitat is necessary for their survival.

Key words: Moapa coriacea, *Moapa dace, life history, reproduction biology, fecundity, age-growth, food habits, habitat use, body size, Muddy River, Nevada.*

The Moapa dace (*Moapa coriacea*) is a thermophilic minnow endemic to the Muddy River system, Clark County, Nevada. First collected in 1938, it has historically been relegated to the headwater area where the Muddy River originates from a series of warm springs (Hubbs and Miller 1948). La Rivers (1962) called the Moapa dace and its coinhabitant, Moapa White River springfish (*Crenichthys baileyi moapae*), thermal endemics because of their apparent affinity for warm water. Rarely exceeding 12 cm in fork length (FL), Moapa dace have morphological similarities to roundtail chub (*Gila robusta*) and speckled dace (*Rhinichthys osculus*), which also inhabit the Muddy River (Hubbs and Miller 1948). They are more similar, however, to the genus *Agosia*, which occurs in other lower Colorado River drainages; the two genera are speculated to have a common ancestor (Hubbs and Miller 1948). Moapa dace are distinguished by small embedded scales and a bright black spot at the base of the caudal fin.

Little was known of Moapa dace life history prior to this study. La Rivers (1962) identified them as methodical schoolers; a cursory gut examination by him indicated that they foraged primarily on arthropods and some vegetative matter. In a systematic sampling effort, Deacon and Bradley (1972) collected Moapa dace in 28–30 C water; one specimen was collected in 19.5 C water. Within the confines of its limited distribution, Moapa dace have been captured in a variety of habitats, including spring pools and slow- to fast-moving water, and in association with various substrates and submergent vegetation (Hubbs and Miller 1948).

Past ichthyofaunal surveys suggested a declining Moapa dace population (Deacon and Bradley 1972, Cross 1976). These surveys were qualitative and produced neither an estimate of the number of dace remaining nor the relative population decrease between surveys. Ono et al. (1984) thought that only several hundred Moapa dace persisted and that their distribution had been further restricted within the already limited historic habitat, confining them to the main stem of the upper Muddy River and a semi-isolated headwater spring system about 130 m long. The purpose of this study is to expand information on Moapa dace life history, abundance, and distribution. Life history information includes reproductive biology, habitat use, food habits, and age and growth.

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STUDY AREA

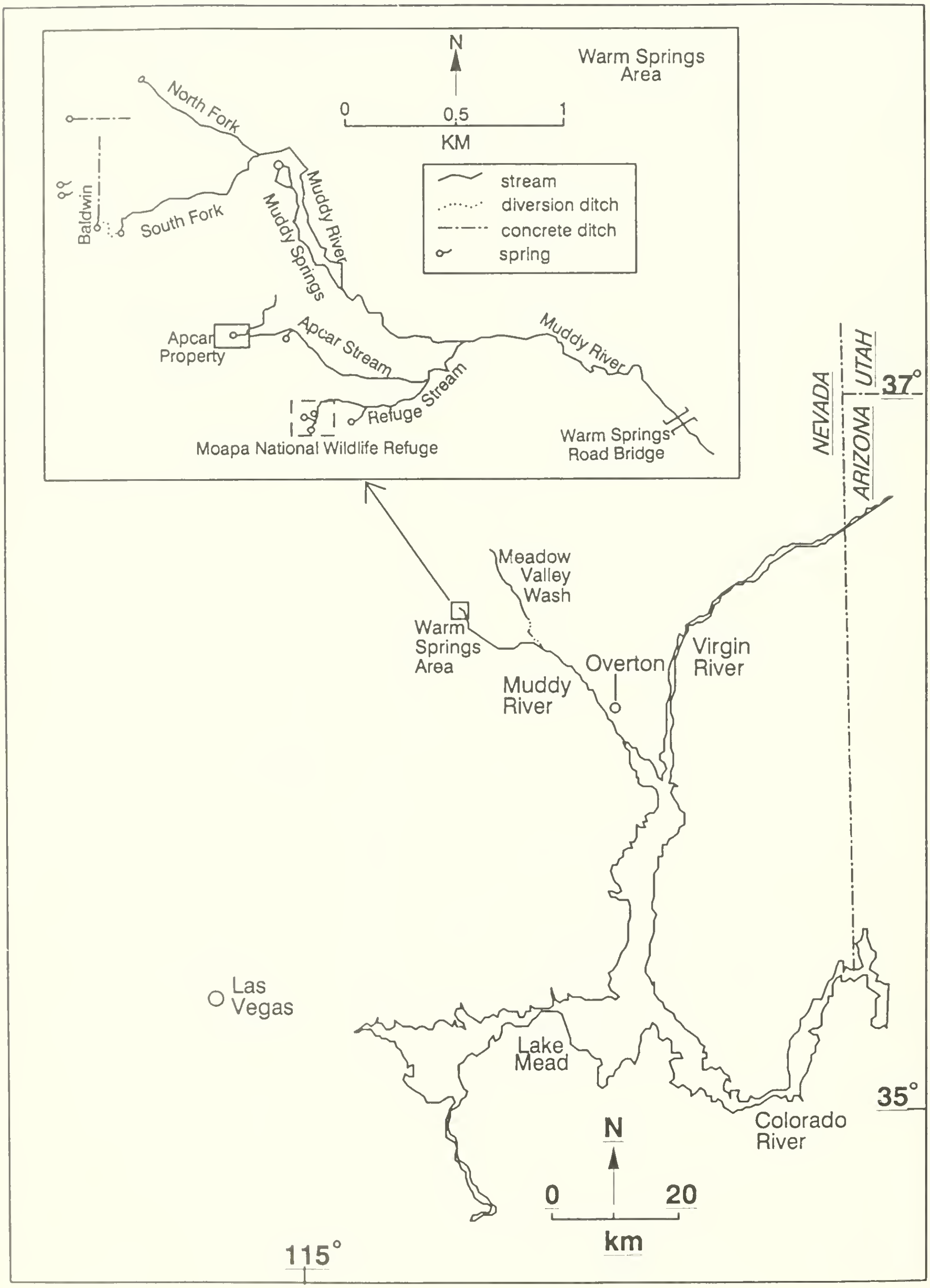
The Muddy River is at the northern edge of the Mohave Desert, where average annual precipitation is 15 cm usually in the form of rain. Carpenter (1915) described historic terrestrial vegetation which included greasewood (*Sarcobatus vermiculatus*), shadscale (*Atriplex confertifolia*), creosote bush (*Larrea tridentata*), and mesquite (*Prosopis* sp.). Stream banks were lined with willows (*Salix* sp.), screw-bean (*Prosopis pubescens*), cottonwood (*Populus* sp.), and mesquite (Carpenter 1915, Harrington 1930). Prior to the completion of Hoover Dam (aka Boulder Dam) in 1935, the Muddy (aka Moapa) River was about 48 km long and discharged into the Virgin River, which joined the Colorado River (Hubbs and Miller 1948). Today, it is about 40 km long and discharges into the Overton arm of Lake Mead (Fig. 1). Source springs of the Muddy River probably originate from Paleozoic carbonate rocks (Garside and Schilling 1979) and occur within a 2-km radius. As is typical of warm springs, the water is relatively rich in minerals. Garside and Schilling (1979) list sodium and calcium as predominant cations, and carbonate and sulfate as predominant anions; total dissolved solids were 854 ppm and pH was 7.7. Water emerges at 32 C and cools and increases in turbidity downstream (Cross 1976). Although spring discharge is relatively constant at about 1.1 m^3/s, the Muddy River flow fluctuates because of rain, agricultural diversions, evaporation, and transpiration (Eakin 1964). The headwater region, the historic range of the Moapa dace, is known as the Warm Springs area (Fig. 1). During our study the area was used primarily for agriculture, and up to 0.25 m^3/s of river discharge was being diverted to irrigate alfalfa, barley, and pasture. Spring outflows had been channelized, and several were converted into irrigation ditches, some lined with concrete. Earthen tributary channels had scant to thick riparian corridors of fan palm (*Washingtonia filifera*), tamarisk (*Tamarisk* sp.), ash trees (*Frazinus* sp.), and arrow weed (*Pluchea sericea*). Two nonnative fishes successfully established in the Warm Springs area: mosquitofish (*Gambusia affinis*), present when Moapa dace were discovered in 1938 (Hubbs and Miller 1948), and shortfin molly (*Poecilia mexicana*), introduced in the early 1960s (Hubbs and Deacon 1964). Besides Moapa dace and springfish, roundtail chub and speckled dace are the only native fishes occurring within the Warm Springs area, but they are rare and in greater abundance downstream (Cross 1976, Deacon and Bradley 1972).

In 1979 the Moapa National Wildlife Refuge (NWR) was established in historic habitat at the southern edge of the Warm Springs area for the preservation and perpetuation of the Moapa dace (Fig. 1). The refuge stream originates from five small springs occurring in a radius of 70 m and having a cumulative discharge of abut 0.09 m^3/s (Fig. 2). Fan palms are the predominant riparian vegetation. In 1984 Moapa dace larvae and adults were reintroduced into the upper Refuge Stream, and by January 1986 there was a stable reproductive population of 120 adults (authors, unpublished data). They were isolated by a 75-cm-high waterfall. Springfish were the only other fish present, and they were abundant.

MATERIALS AND METHODS

REPRODUCTIVE BIOLOGY.—Among our objectives was to quantify duration of the reproductive period and the season of peak larvae recruitment. To this end, a segment of the upper Refuge Steam system was snorkeled at 30- to 90-day intervals from February 1986 to January 1989 and larvae were enumerated (Fig. 2). This is the area in which virtually all reproduction on the Moapa NWR occurred. Dace 7–15 mm TL were considered larvae. This range approximates the proto- to metalarvae stages of the similar-sized speckled dace (Snyder 1981). Snorkeling enabled us to locate reproduction sites in the headwater Muddy River system and to determine the abundance and distribution of adult Moapa dace as well as to quantify habitat use for all life stages. Areas with larvae close to swim-up size (about 7 mm TL) were considered reproduction sites. Fish used for food habit analysis and aging were also used to determine fecundity.

HABITAT USE.—We defined habitat use in terms of stream depth and velocity at foraging sites and at suspected spawning areas. Depth measurements included focal and total, while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Muddy River
Refuge Stream
Moapa National Wildlife Refuge
Warm Springs Road Bridge
NEVADA
UTAH
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37°
Meadow Valley Wash
Warm Springs Area
Overton
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Muddy River
Las Vegas
Lake Mead
Colorado River
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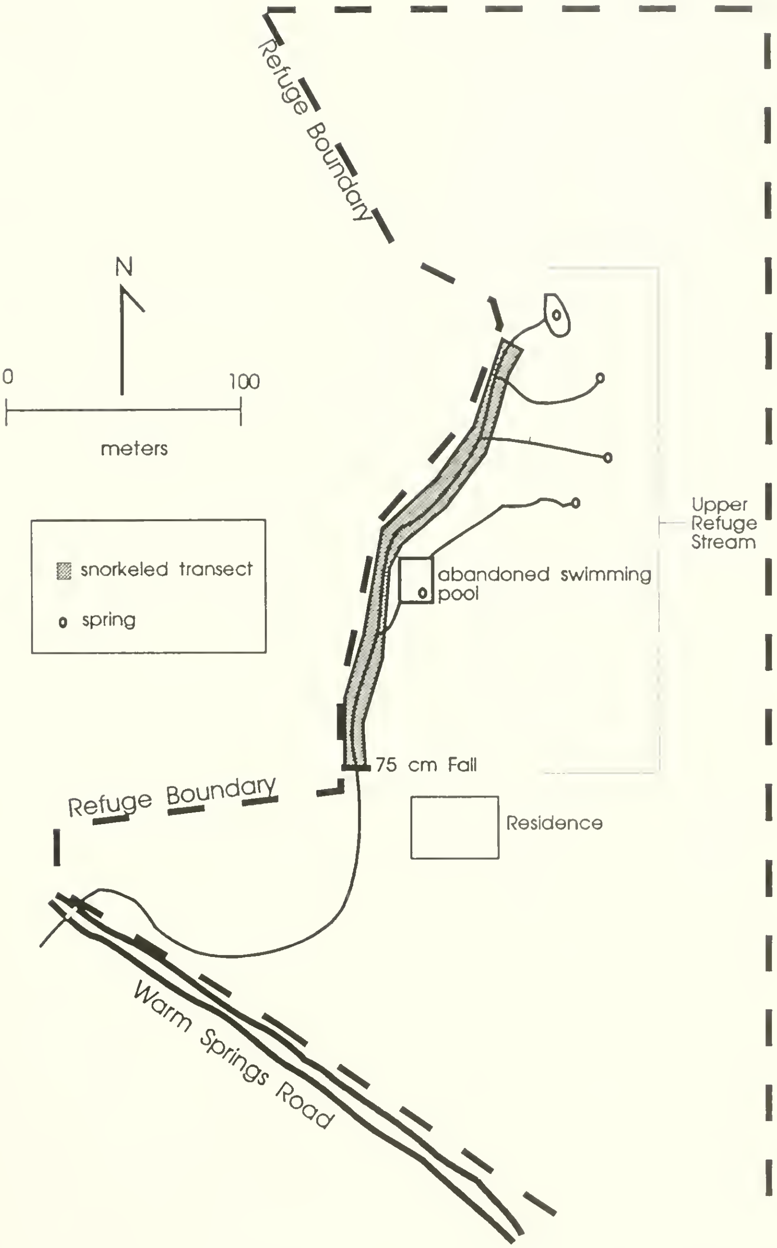
Fig. 1. Map showing relationship of the Muddy to the Virgin River and Lake Mead, Nevada, and relationship of the Warm Springs area to the Muddy River (below). Warm Springs area or headwaters of the Muddy River showing tributary streams to the upper Muddy River and relationship of the Moapa National Wildlife Refuge (above).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▨ snorkeled transect
o spring
Upper Refuge Stream
abandoned swimming pool
75 cm Fall
Refuge Boundary
Residence
Warm Springs Road

Fig. 2. Map of Moapa National Wildlife Refuge; shaded site indicates the reach of the upper Refuge Stream where larvae snorkel counts were made from February 1986 to January 1989.

velocity measurements included focal and mean water column, as prescribed by Bovee (1986). Dissolved oxygen and temperature were also measured. Fish were located using mask and snorkel. A Marsh and McBirney model 201D digital flow meter mounted on a calibrated rod was used to measure depth and velocity, and a Yellow Springs Instrument model 57 dissolved oxygen meter for temperature and dissolved oxygen. Sampling occurred from 1984 to 1986. Adult habitat was also defined by contrasting body size with quantity of stream flow; it was our subjective evaluation that larger fish were inhabiting larger water volumes. We tested this

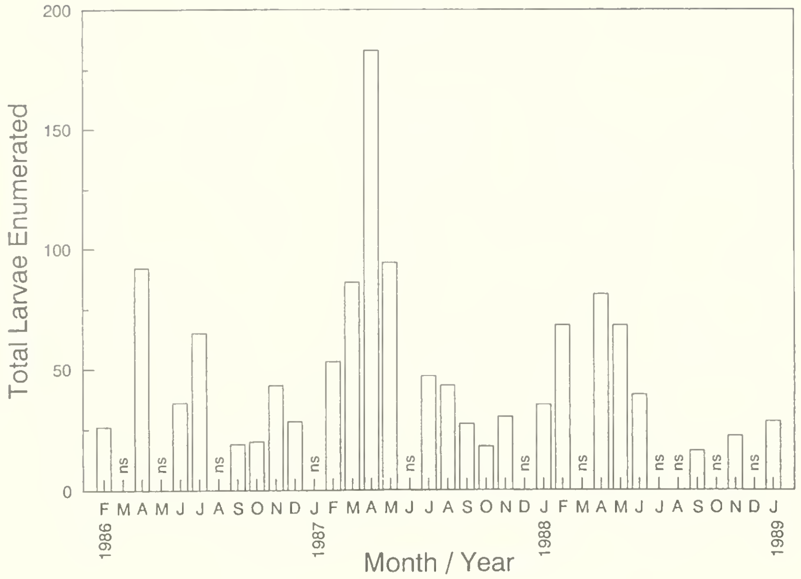

Fig. 3. Abundance of Moapa dace larvae from February 1986 to January 1989 in the Muddy River system on the Moapa National Wildlife Refuge, Nevada. Bars represent a single day's count for the month. NS indicates not sampled.

hypothesis in the summer of 1986 when samples of adults were minnow-trapped from the Muddy River, Muddy Spring Stream, Refuge Stream, and Apcar Stream and their length frequencies compared. Discharge for each stream was measured using standard U.S. Geological Survey methods (Rantz et al. 1982) near each fish sample. A one-way factorial ANOVA was used to test whether there was a significant difference between length frequency among fishes and different water volumes.

AGE AND GROWTH.—The opercle bone was used for estimating age as described by Casselman (1974). Eight specimens, collected in summer 1985 and 1986, were aged. Flesh was scraped with a scalpel and the bone allowed to dry. Glycerin was used to highlight the more transparent region of the bone, which was assumed to have the greatest calcium concentration and to have been formed in the winter when food is scarce. The more opaque region signifies greater concentration of protein associated with growth (Casselman 1974).

FOOD HABIT.—Food habit analyses were made from 10 Moapa dace taken 9–11 November 1984 from each of three upper Muddy River tributaries (Apcar, South Fork, and Muddy Spring). They were captured by seining and with unbaited minnow traps fished no longer than 10 minutes. Ranging from 42 to 71 mm FL, they were preserved in 10% formalin solution. Contents in the anterior third of the gut were examined using a dissecting microscope and quantified by frequency of occurrence (Windell 1971) and by percent composition (Hynes 1950).

ABUNDANCE AND DISTRIBUTION.—The abundance and distribution of adult Moapa dace (>40 mm FL) were determined by snorkeling the upper Muddy River system beginning from 200 m downstream of Warm Springs Road bridge (Fig. 1). Except for 1984, the surveys included 5.3 km of the upper Muddy River and 7.5 km of its spring-fed tributaries (Refuge Stream system, Apcar Stream, Muddy Spring, South Fork, and North Fork). In 1984 the survey area was the same except that only the upper 130 m of the Apcar Stream was snorkeled rather than its entire stream length. Snorkeling was conducted over periods of four to six days when turbidity was low (between 1.4 and 5.0 NTU) because no agricultural return flows were entering the stream. Counts were made 6–10 December 1984, 6–10 June 1986, and 16–22 September 1987. Each observer enumerated Moapa dace twice at three areas of relatively high concentrations (30–60 fish), and the range of results was then calculated. These sites were chosen because the greatest variation among observers was expected among them. For the three sites, variation was less than 15% in counts

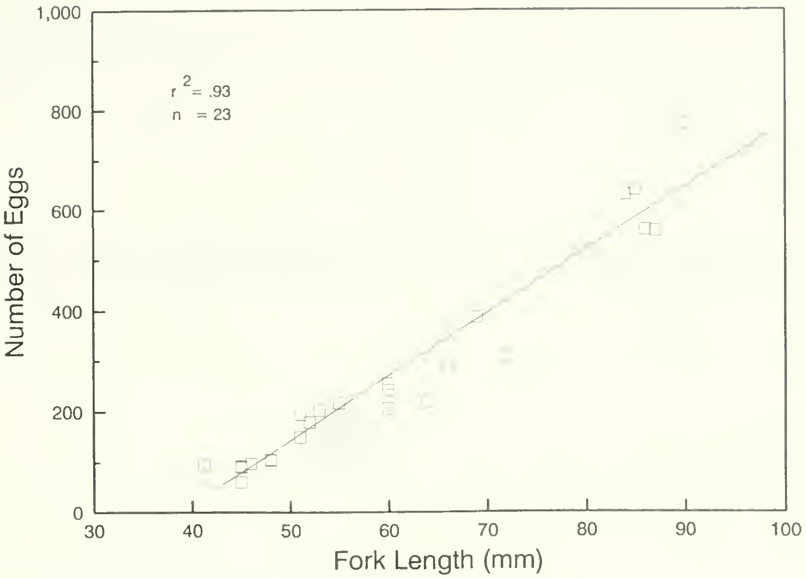

Fig. 4. Moapa dace fecundity as a function of fork length.

between individuals; thus, we conservatively estimated a 15% variation in our population counts.

RESULTS AND DISCUSSION

Reproductive Biology

Moapa dace larvae were found year-round, indicating year-round reproduction. On the Moapa NWR peak larval recruitment was in spring, the low in autumn (Fig. 3). Fish at other reproductive sites in the Warm Springs area exhibited this same general trend. Seasonal fluctuation in larval recruitment was probably linked to availability of food. In the upper Muddy River system the abundance of benthic and drifting invertebrates is much lower in winter than in spring (Scoppettone, unpublished data). Naiman (1976) documented substantial seasonal fluctuation in primary productivity in another southwestern warm springs where production is lowest in winter; presumably most invertebrate population fluctuates with primary production.

Recently emerged larvae were found within 150 m of spring discharge over sandy silt bottoms in temperatures of 30–32 C and dissolved oxygen of 3.8–7.3 mg/L. Whether spawning occurs only at these headwater sites or is successful only at these sites is unknown. Visual cues such as sexual dichromatism, pronounced male spawning tubercles, or overtly gravid females were not readily apparent, and spawning was not observed during our study. However, we indirectly identified and quantified spawning habitat. The presence of hundreds of protolarvae in a concrete irrigation channel immediately downstream of the Baldwin springhead (Fig. 1) indicated that reproduction had taken place. Progenitors apparently came from the South Fork, entering Baldwin Spring outflow through a diversion channel (Fig. 1). The concrete irrigation channel had homogeneous water depth and velocity, and substrate was sandy silt. Several depressions in the sand were similar to "redds" described for longfin dace (*Agosia chrysogaster*; Minckley and Willard 1971). Depth and velocity at the suspected redds were representative of the outflow channel and similar to other suspected spawning areas in the Warm Springs area. Depth ranged from 15.0 to 19.0 cm, near-bed velocities from 3.7 to 7.6 cm/sec, and mean water column velocity from 15.2 to 18.3 cm/sec.

Similar to the longfin dace, which reproduces during much of the year (Kepner 1982), eggs in the skein of Moapa dace were in different stages of development. All visible eggs were counted, but because they are intermittently deposited and develop throughout a given year, our counts do not represent absolute annual fecundity. However, egg production increased with fish size (r^2 = .93, n = 25; Fig. 4). Counts

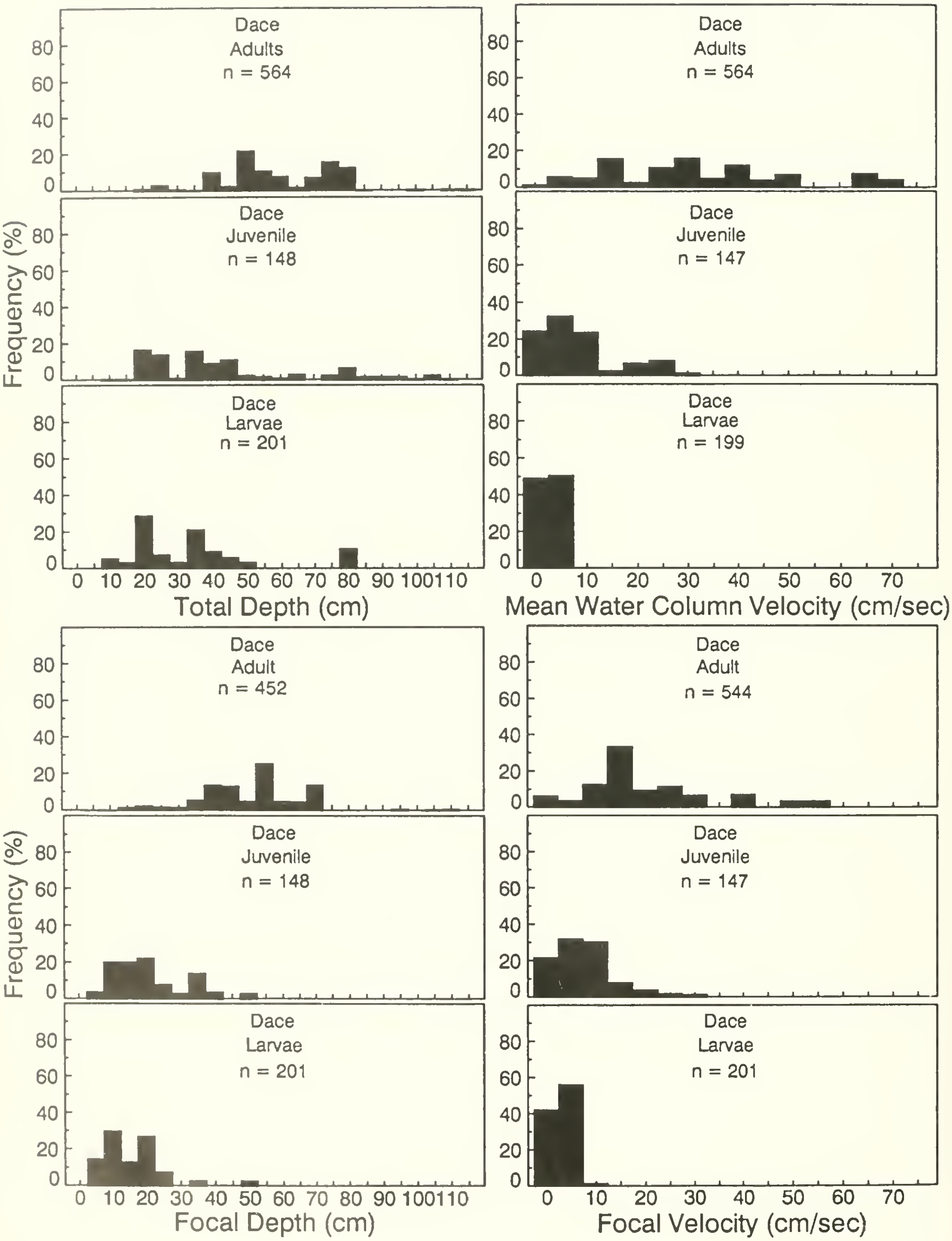

Fig. 5. Mean water column and focal point velocities, total depth, and focal point depth used by Moapa dace adults, juveniles, and larvae in the upper Muddy River system (Warm Springs area), Nevada, 1984 through 1986.

TABLE 1. Fork length, sex, and estimated age of eight Moapa dace collected from the upper Muddy River system, Nevada, in 1985 and 1986. Age was determined by the opercle method.

FL (mm)	Sex	Collection date	Age
45	Unknown	4/86	0+
55	Unknown	7/86	1+
61	Unknown	7/86	1+
67	Female	4/86	2+
69	Female	04/22/86	2+
77	Unknown	10/09/85	3+
80	Unknown	10/11/85	3+
90	Female	10/08/85	4+

TABLE 2. Food items ingested by 21 Moapa dace by percent composition (Hynes 1950) and percent frequency of occurrence (Windell 1971). Nine other guts examined were empty.

Food items	% composition	% of occurrence
GASTROPODA		
Tyronia clathrata	1.1	4.8
OLIGOCHAETE	27.0	23.8
AMPHIPODA		
Hyallela azteca	1.7	9.5
HEMIPTERA		
Pelocoris shoshone	4.5	4.8
HOMOPTERA		
Aphiidae	9.0	4.8
TRICHOPTERA		
Dolophilodes	5.1	9.5
Nectopsyche	4.5	9.5
LEPIDOPTERA		
Paragyractis	4.5	9.5
COLEOPTERA		
Stenelmis calida	1.1	4.8
Dytiscidae (larvae)	9.0	4.8
DIPTERA		
Chironomidae	4.5	4.8
Unidentified insect parts	3.3	9.5
Filamentous algae	18.5	42.3
Vascular plants	3.4	9.5
Detritus	2.8	14.3

ranged from 60 in a 45-mm-FL individual to 772 in a 90-mm-FL dace. Eggs were just developing in a 41-mm-FL female and were mature in a 45-mm-FL fish, suggesting that females mature at lengths in this range.

Habitat Use

Again, Moapa dace larvae were found exclusively in the upper reaches of spring-fed tributaries, while juveniles occurred primarily in tributaries but were more far-ranging. Adults were present in tributaries and in the main river, with larger fish generally found in the larger water volumes. There were significant differences in length frequencies among adults from different water volumes ($p \leq .006$). In the Muddy River, in a flow of about 0.50 m^3/s, mean FL was 73 mm (n = 78, SD = 16 mm); Muddy Spring had a flow of 0.20 m^3/s, and the mean FL was 64 mm (n = 72, SD = 14 mm); the Refuge Stream flowed at 0.17 m^3/s, and mean FL was 56 mm (n = 64, SD = 8 mm); the Apcar Stream flowed at 0.06 m^3/s, and mean FL was 51 mm (n = 89, SD = 5 mm).

Larvae occurred and fed in the mid- to upper region of the column. They were found most frequently in zero water velocity (Fig. 5). As size increased, individuals tended to occupy faster water and occur lower in the water column. Juvenile Moapa dace occupied focal and mean water column velocities ranging from 0 to 46 cm/s. Adults were found in a wide range of water depths and velocities, but they tended to orient at the bottom in low to moderate current. Water column depth ranged from 15 to 113 cm and focal point depth from 9 to 107 cm. Mean water column velocity ranged from 2 to 77 cm/s and focal point velocity from 0 to 55 cm/s. Water temperatures within adult habitats ranged from 27 to 32 C and dissolved oxygen from 3.5 to 8.4 mg/L.

Age Growth

Annulus formation is typically associated with an annual period of slower growth caused by seasonal changes in environmental conditions such as temperature or food resources (Tesch 1971). Although seasonal water temperatures do not change substantially in the Warm Springs area, there is an apparent reduction of potential food during the winter (Scoppettone, unpublished data). We were unsuccessful in aging Moapa dace by the scale method because scales were small, embedded, and extremely difficult to remove from live specimens. Also, environmental conditions in waters of the Warm Springs area were sufficiently constant that annuli were not readily apparent. Assumed annuli on opercular bones were presumed to be associated with slower growth during the winter. Ages of the eight fish examined ranged from 0+ for a 43-mm-FL individual to 4+ for a 90-mm-FL female (Table 1).

Food Habit

Nine of 30 guts examined were empty and the remainder generally contained few items.

TABLE 3. Estimated number of Moapa dace adults in six tributary streams in the Warm Springs area, Muddy River system, Nevada, 6–14 December 1984, 13–18 June 1986, and 16–22 September 1987.

Stream name	December 1984	Variation in count	June 1986	Variation in count	September 1987	Variation in count
Muddy River	475	±71	1230	±185	1165	±175
Refuge System	370	±56	406	±61	806	±121
Apcar	200	±30	565	±85	475	±72
South Fork	300	±45	185	±28	100	±15
North Fork	15	±2	30	±5	60	±9
Muddy Spring	1450	±218	160	±24	200	±30
Total	2810	±422	2581	±387	2806	±421

[1] Only the upper 130 m of stream was sampled in 1984

but what had been consumed indicated Moapa dace to be omnivorous tending toward carnivory; 75% by composition was invertebrates while 25% was plant material and detritus (Table 2). Among 21 dace guts, oligochaetes represented the largest volume (27.0%) of foodstuffs consumed, followed by filamentous algae (18.5%). In terms of frequency of occurrence filamentous algae occurred in 42.3% of the guts while oligochaetes were in 23.8%. The structure of the pharyngeal teeth also suggests an omnivorous diet; they are strongly hooked but have a well-developed grinding surface (La Rivers 1962). The presence of detritus and gastropods indicates at least some foraging from the benthos, and we observed fish in the field occasionally pecking at substrate. However, the greatest time in foraging is expended on drift feeding (authors, unpublished data), although our data set does not strongly support this observation.

Abundance and Distribution

Moapa dace were more widespread and numerous than had been previously reported (Ono et al. 1984); they were in five headwater tributaries and the upper Muddy River to about 100 m downstream from the Warm Springs Road bridge (Fig. 2). Numbers ranged from about 2600 in 1986 to 2800 in 1984 and 1987. The numerical distribution for the three years suggests movement by the adult population (Table 3). In 1984 the Muddy Spring stream supported about 50% of the population (1450 adults), with only 16% (450 adults) found in the river. In June 1986 we could account for only 7% of the population in the Muddy Spring stream, while almost 50% of the total was in the river. In 1987 the mainstream river again supported most adult Moapa dace (1200). The distribution of adult Moapa dace was patchy and clumped. For example, during the snorkel survey in summer 1986, 79% of the observed dace in the main stem Muddy River were in groups of 10 or more, and 37% were in groups of 30 or more. In tributaries, groups were generally smaller, with 52% of the adults in groups of 10 or more and only 13% in groups of 30 or more.

CONCLUSION

Moapa dace are dependent upon the link between the upper river and its tributaries. The main stem river typically harbors the largest, and presumably the longest-lived, and most fecund fish; yet tributaries are important for reproduction and as larvae and juvenile nursery habitat. Age and growth information suggests that three years is the mean age of fish in the river and that adults in smaller tributaries are one to two years old.

Although the Moapa dace population is more widespread and abundant than previously believed, its existence remains in jeopardy. Widespread movement and obligatory spawning near warm water spring discharge suggest that species survival depends on access to the entire headwater Muddy River system (Warm Springs area), river and tributaries alike. Every effort should be made to preserve all of its remaining habitat.

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CONDITION MODELS FOR WINTERING NORTHERN PINTAILS IN THE SOUTHERN HIGH PLAINS

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ABSTRACT—Three condition models for wintering Northern Pintails (*Anas acuta*) were tested for their ability to predict fat mass, logarithm of fat mass, or a condition index (CI) incorporating fat mass. Equations generated to predict fat mass and the logarithm of fat mass accounted for more than 69% of the variation in these dependent variables. Log transformations of body mass, wing length, and total length explained at least 60% of the variation in CI. All models performed better on an independent data set. Mean prediction error was minimal (≤8% of measured variables) and negative for all models. Regression models apply to live and dead pintails and thus represent tools that have utility in a wide variety of studies on pintail condition.

Key words: Northern Pintails, Anas acuta, *body condition, predictive models, Texas, waterfowl.*

Biologists have used various indices for assessing waterfowl nutritional status. Initially, only body mass was used (Hanson 1962, Folk et al. 1966, Street 1975, Flickinger and Bolen 1979), but later structural variables were incorporated to adjust for individual size differences (Owen and Cook 1977, Bailey 1979, Wishart 1979). Ringelman and Szymczak (1985) and Johnson et al. (1985) reviewed avian condition indices and noted the value of an accurate index of lipids in migratory bird management. These studies noted that scaling morphological variables with body mass provided useful indices to avian body condition.

Northern Pintails (*Anas acuta*) are one of the most widespread waterfowl species in North America (Bellrose 1980), but recently their populations have declined, making them a species of special concern (Smith et al. 1991). Our objectives were to provide an equation to predict total carcass fat (body condition) of Northern Pintails and to test that index on an independent data set. The anatomical variables tested are suitable for field studies.

STUDY AREA

The study was conducted in the Southern High Plains (SHP) of Texas, an 82,880-km^2 area that is one of the most intensively cultivated regions in the Western Hemisphere (Bolen et al. 1989). Twenty thousand playas are present in the SHP providing winter habitat for waterfowl (Haukos and Smith 1992). At least one-third (≥300,000) of the Northern Pintails wintering in the Central Flyway winter on the SHP (Bellrose 1980).

METHODS

Northern Pintails were collected using decoys and by jump-shooting on playas and associated tailwater pits in the SHP from October through March of 1984–85 and 1985–86. Tarsal length (measured from the junction of the tibiotarsus and tarsometatarsus to the point of articulation between the tarsometatarsus and middle toe, 0.01 mm), flattened wing chord (measured from the insertion of the alula to the tip of the tenth primary, 0.1 cm), and total body length (measured from the tip of the bill to the end of the pygostyle, thus avoiding complications due to tail feather growth, 0.1 cm) were recorded for each bird. During 1985–86 an additional wing measurement was recorded from the insertion of the alula to the tip of the ninth primary because the ninth primary may be slightly longer than the tenth. Birds were plucked and frozen.

Ingesta and intestinal contents were removed in the laboratory. Birds then were

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TABLE 1. Variables used in predictive models of body condition for Northern Pintails (*Anas acuta*) on the Southern High Plains, Texas.

Variable	Adult males (n = 140) $\bar{x}$	SE	Adult females (n = 69) $\bar{x}$	SE	Juvenile males (n = 58) $\bar{x}$	SE	Juvenile females (n = 49) $\bar{x}$	SE
Mass (g)	963.93	10.94	835.07	12.60	911.97	16.41	786.68	14.90
Tarsal length (mm)	41.15	0.17	38.68	0.23	41.13	0.25	38.90	0.30
Wing length (cm)	26.58	0.06	24.69	0.08	25.92	0.10	24.23	0.09
Total length (cm)	49.72	0.12	43.37	0.14	49.53	0.22	43.14	0.19
Lipid mass (g)	171.57	6.27	173.20	8.33	147.93	11.07	148.21	9.56

reweighed (nearest 0.01 g) to determine a net carcass mass and refrozen (Table 1). Frozen birds were sectioned with a meat saw and passed twice through a meat grinder. The homogenate was dried to a constant mass in either a forced-air oven (60 C) or freeze dryer. Dried pintails were reground to insure a uniform mixture. Lipid was extracted from 10–15 g samples using petroleum ether solvent in a Soxhlet apparatus (36–48 hrs). Fat-free dry mass (FFDM) was calculated by subtracting water and lipid from total carcass mass (body mass minus feathers and ingesta). Total carcass mass minus water mass yielded dry mass (DM).

Three models were evaluated to predict (1) fat mass, (2) a condition index (CI) incorporating fat mass, and (3) the logarithm of fat mass of wintering Northern Pintails. First, pintails were sorted by sex (age was not significant; multiple regression, $P > .05$). A predictive model for fat was generated for each sex using total body length (TOTAL), wing length (WING), tarsal length (TARSAL), and body mass (MASS) as explanatory variables.

In model 1, regression coefficients of explanatory variables between sexes were not different ($P > .05$). A predictive equation applicable to both sexes was therefore constructed which included a dummy variable for sex (DSEX) as well as structural variables.

The second model was constructed following Johnson et al. (1985); a Lipid Index was defined:

$$\text{Lipid Index} = \text{Fat} / \text{FFDM}.$$

Fat-free dry mass is included to correct for size differences between individuals. Lipid Index was transformed to:

$$\text{CI} = \log(\text{Lipid Index} + 1)$$

because the structural measurements are allometric and because logarithms can be used to linearize ratios (Johnson et al. 1985). The constant 1 was added to smooth the function. CI can be simplified to:

$$\text{CI} = \log(\text{DM}/\text{FFDM})$$

because

$$\text{DM} = \text{Fat} + \text{FFDM}.$$

Log FFDM was modeled as a function of the logarithms of structural variables (LTOTAL, LWING, and LTARSAL) and log DM as a function of these plus the logarithm of body mass (LMASS) (Johnson et al. 1985). Unlike Mallards (*Anas platyrhynchos*; Ringelman and Szymczak 1985) and Canada Geese (*Branta canadensis*; Raveling 1979), water content of wintering Northern Pintails fluctuated widely (Smith and Sheeley 1993). Therefore, we did not test fat-free mass as an index to structural size (Ringelman and Szymczak 1985).

Johnson et al. (1985) used logarithms of structural variables to model logarithms of carcass fat mass (log fat). A separate equation was estimated for each age/sex group (model 3) using dummy variables for age (DAGE) and sex (DSEX) because regression coefficients for explanatory variables differed ($P < .05$) among these four groups.

Predictive equations were validated on a data set of 40 randomly selected pintails not included in the generation of models. Percentages of each age/sex class of pintails in the independent sample were consistent with their occurrence in the sample collection.

Prediction error (PE) was calculated as an additional test of model performance. PE is defined as:

$$\text{PE} = \text{Measured Y} - \text{Predicted Y}$$

where Y is the dependent variable. Mean PE is an average value for all members of the validation data set. Finally, predicted fat, CI, and log fat were correlated with Lipid Index in the validation data.

TABLE 2. Regression equations and associated statistics for predicting carcass fat (model 1) content (g) in Northern Pintails (*Anas acuta*) collected on the Southern High Plains of Texas, October–March 1984–86.

			Explanatory variables				
Equation	R^2		Intercept	MASS	WING	TOTAL	DSEX
1.1	.779	Parameter estimate	191.854	0.560	−13.386	−4.136	—
(Male; $n = 198$)		SE	—	0.022	3.894	1.901	—
		Variance inflation factor	—	1.181	1.231	1.221	—
		Partial R^2	—	0.741	0.013	0.005	—
1.2	.711	Parameter estimate	145.570	0.570	−9.516	−4.953	—
(Female; $n = 118$)		SE	—	0.035	5.561	2.994	—
		Variance inflation factor	—	1.125	1.212	1.174	—
		Partial R^2	—	0.691	0.007	0.007[a]	—
1.3	.757	Parameter estimate	190.494	0.563	−12.068	−4.409	−22.513
(Combined; $n = 316$)		SE	—	0.018	3.178	1.600	10.536
		Variance inflation factor	—	1.492	3.164	6.842	5.987
		Partial R^2	—	0.726	0.011	0.006	0.004

[a] Not significant ($P > .05$)

TABLE 3. Regression equations and associated statistics for predicting Condition Index (model 2) in Northern Pintails (*Anas acuta*) collected on the Southern High Plains of Texas, October–March 1984–86.

			Explanatory variables				
Equation	R^2		Intercept	LMASS	LWING	LTOTAL	DSEX
2.1	.673	Parameter estimate	−0.816	1.371	−1.025	−0.909	—
(Male; $n = 198$)		SE	—	0.069	0.343	0.312	—
		Variance inflation factor	—	1.190	1.233	1.229	—
		Partial R^2	—	0.656	0.015	0.014	—
2.2	.599	Parameter estimate	−0.725	1.316	−1.179	−0.710	—
(Female; $n = 118$)		SE	—	0.101	0.512	0.486	—
		Variance inflation factor	—	1.123	1.206	1.176	—
		Partial R^2	—	0.595	0.019	0.008	—
2.3	.657	Parameter estimate	−0.761	1.350	−1.080	−0.834	−0.041
(Combined; $n = 316$)		SE	—	0.057	0.286	0.264	0.016
		Variance inflation factor	—	1.496	3.207	7.035	6.141
		Partial R^2	—	0.610	0.016	0.011	0.007

Stepwise multiple regression (maximum R^2 improvement technique) was used to generate and test all models (SAS Institute, Inc. 1985). Variables were eliminated that did not contribute significantly ($P < .05$) to a model. Partial R^2 values were calculated for each variable in a model. A sum of squares (Type II) for each model variable was divided by the total sum of squares in the model. A partial R^2 value for a given variable represents the unique contribution of that variable when all other variables are already present in the model. Partial R^2 values are not additive, and, therefore, their sum will not equal the total model R^2. Differences in variation accounted for by ninth versus tenth primary length were evaluated using the R^2 procedure (SAS Institute, Inc. 1985).

RESULTS

In model 1 (Table 2) body mass explained a major portion of variation in carcass fat content in males (equation 1.1) and females (equation 1.2). Total length did not account for a significant ($P > .05$) portion of variation in fat content for females as it did males. Based on low variance inflation factors (VIF), regression coefficient estimates for each sex were stable. When sexes were combined through use of a dummy variable (equation 1.3), the VIF for TOTAL and DSEX were relatively high; this is largely attributable to the high correlation between length and sex of bird (point biserial correlation coefficient equal to 0.91).

LTOTAL, LWING, and LTARSAL explained variation in log FFDM. For modeling,

TABLE 4. Regression equations and associated statistics for predicting log carcass fat (model 3) in Northern Pintails (*Anas acuta*) collected on the Southern High Plains of Texas, October–March 1984–86.

				Explanatory variables	
Equation	R^2		Intercept	LMASS	LWING
3.1	.727	Parameter estimate	−3.410	3.412	−3.209
(Adult male; n = 140)		SE	—	0.182	0.993
		Variance inflation factor	—	1.156	1.156
		Partial R^2	—	0.697	0.021
3.2	.693	Parameter estimate	−1.611	3.687	−4.998
(Adult female; n = 69)		SE	—	0.303	1.472
		Variance inflation factor	—	1.034	1.034
		Partial R^2	—	0.687	0.054
3.3	.722	Parameter estimate	−11.066	5.028	−1.223
(Juvenile male; n = 58)		SE	—	0.422	2.009
		Variance inflation factor	—	1.015	1.015
		Partial R^2	—	0.719	0.002
3.4	.745	Parameter estimate	−5.444	3.968	−2.834
(Juvenile female; n = 49)		SE	—	0.348	1.844
		Variance inflation factor	—	1.109	1.109
		Partial R^2	—	0.720	0.013

TABLE 5. Coefficients of determination (R^2) and predictive error estimates from the validation (n = 40) of predictive equations to measured variables and Lipid Index for wintering Northern Pintails (*Anas acuta*) on the Southern High Plains of Texas, October–March 1984–86.

Equation	R^2	Mean prediction[a] error (± SE)	Lipid Index R^2
1.1 and 1.2	.785	−9.921 ± 5.850[b]	.662
(fat)		6.16%	
1.3	.765	−9.043 ± 5.853	.659
(fat)		6.24%	
2.1 and 2.2	.697	−0.0192 ± 0.0091	.671
(Condition Index)		7.87%	
2.3	.700	−0.019 ± 0.0092	.675
(Condition Index)		7.79%	
3.1–3.4	.733	−0.050 ± 0.0009	.634
(log fat)		2.41%	

[a] Prediction error expressed as a percentage of the mean in the validation data set.

[b] Negative prediction error indicates overestimation of the true value

log DM, LMASS, LWING, and DSEX were significant ($P < .05$). Thus, CI was modeled with LTOTAL, LWING, LTARSAL, and LMASS for sexes separately and combined (Table 3). As in model 1, regression coefficient estimates were stable in equations 2.1 and 2.2; when sexes were combined, multicollinearity between TOTAL and DSEX resulted in relatively high VIFs for these variables.

Age and sex effects were significant when log fat was regressed on the same explanatory variables used in model 2. Furthermore, the structural variables LMASS and LWING were the only variables that contributed significantly ($P < .05$), but they were not homogeneous ($P < .05$) between age/sex groups. Therefore, four equations were estimated (Table 4). DAGE explained variation in log fat but not CI.

Given other model variables, body mass (MASS and LMASS) consistently accounted for the largest portion of variation in carcass fat (Table 2), CI (Table 3), and log fat (Table 4) of wintering Northern Pintails. Wing length (WING and LWING) explained 1–5% of the variation in carcass fat, log fat, and CI when other variables were already in the models. TARSAL did not contribute to any model. Variation accounted for by ninth and tenth primary lengths always differed by less than 1%. Consequently, ninth primary length was not tested in any model.

In the validation data set all models accounted for 69% or more of variation in carcass fat mass, CI, and log fat (Table 5). All models explained less than 70% of the variation in Lipid Index for validation data-set birds. Bias in all models was relatively low and negative. Predictive equations overestimated fat mass, CI, and log fat of validation data-set pintails.

DISCUSSION

A useful condition index will save funds by eliminating the need for expensive laboratory analyses and will lessen the need to sacrifice birds for direct nutrient analyses. The problems associated with using body mass alone as an index to condition of migratory birds have been noted (Bailey 1979, Wishart 1979, Iverson and Vohs 1982, Johnson et al. 1985). Because individuals vary in structural size, body mass will reflect that variability in muscle and bone, in addition to variation in lipids.

Models have been developed that predict fat content in waterfowl, but these require sacrifice and dissection of the bird (Woodall 1978, Chappell and Titman 1983, Thomas et al. 1983, Whyte and Bolen 1984). These equations may incorporate skin (subcutaneous), abdominal (omental), and/or intestinal (visceral) fat mass, and often account for most of the variation in total body-fat content. Our study was designed to develop models using explanatory variables that could be applied to live as well as dead pintails.

Miller (1989) developed regression models to predict carcass fat on live pintails from Sacramento Valley, California, but cautioned against their use outside that region. Our regression models for carcass fat provided better estimates of fat ($R^2 > .71$) for live pintails than those developed for California birds ($R^2 \leq .66$). However, similar to Miller's (1989) study, body mass alone accounted for most of the variation ($R^2 > .69$) in pintail carcass fat.

The possibility of a condition bias among waterfowl captured in baited traps versus the general population has been addressed (Weatherhead and Ankney 1984, 1985, Burnham and Nichols 1985). Hypothetically, birds in poor condition may be hungrier, less wary, and more likely to enter a trap containing food. Condition models could be used to test for evidence of a body-condition bias, given that samples of pintails captured both in baited traps and by presumably less-biased methods (e.g., net gun) are available.

Models could be used to test for annual variation in body condition and for changes in condition across the winter. Ringelman and Szymczak (1985) demonstrated the potential of condition indices in determining spatial differences in body condition and the preferability of condition indices to use of body mass alone. Hepp et al. (1986) also used condition indices to document a positive relationship between condition and survival in mallards.

These pintail condition models should be useful to waterfowl biologists. However, models should be verified when used outside the geographical range in which they were developed. For comparisons between age and sex classes we encourage use of model 3. Research also may require knowledge of absolute fat content. Importance of accuracy and precision will affect model selection. Care should be exercised to restrict model use to winter when changes in body mass primarily reflect fluctuations in fat, not fat-free dry mass (i.e., protein and mineral fractions).

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EVALUATION OF ROAD TRACK SURVEYS FOR COUGARS (*FELIS CONCOLOR*)

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ABSTRACT.—Road track surveys were a poor index of cougar density in southern Utah. The weak relationship we found between track-finding frequency and cougar density undoubtedly resulted in part from the fact that available roads do not sample properly from the nonuniformly distributed cougar population. However, the significantly positive relationship ($r^2 = .73$) we found between track-finding frequency and number of cougar home ranges crossing the survey road suggested the technique may be of use in monitoring cougar populations where road abundance and location allow the population to be sampled properly. The amount of variance in track-finding frequency unexplained by number of home ranges overlapping survey roads indicates the index may be useful in demonstrating only relatively large changes in cougar population size.

Key words: cougar, Felis concolor, *track survey, Utah.*

Sign left by animals has been commonly used by wildlife managers to make inferences about population characteristics (Neff 1968, Lindzey et al. 1977, Novak 1977). This approach is appealing because it seldom requires specialized equipment and is usually much less costly than other, more intensive techniques. The approach requires, however, that the relationship between sign and the population characteristic of interest (e.g., size, composition) be understood.

Track counts have been used to indicate cougar (*Felis concolor*) abundance or change in abundance, but population estimates were seldom available to evaluate the validity of these indices (Koford 1978, Shaw 1979, Fitzhugh and Smallwood 1988). Van Dyke et al. (1986), however, conducted road track surveys in an area of known cougar density and found a weak relationship ($r^2 = .18$) between track-finding frequency and density. Because of the potential value of this technique to agencies charged with management of cougars, our objective was to test again the relationship between track-finding frequency and cougar density following procedures of Van Dyke et al. (1986). Additionally, we examined the influence cougar distribution patterns, as measured by cougar home ranges, had on track-finding frequency.

STUDY AREA

The Boulder-Escalante study area comprises 4500 km^2 of Garfield and Kane counties in south central Utah. Boulder, Escalante, and Canaan mountains dominate the area topographically, and elevation ranges from 1350 m to 3355 m. Hot, dry weather is characteristic of June and July, with rains beginning in August and continuing through September. Annual precipitation ranges from 18 cm at low elevations to 60 cm at high elevations; average temperatures for Escalante in January and July are −2.8 C and 24.5 C, respectively (U.S. Department of Commerce 1979).

Desert grass and shrub communities dominate the vegetation with a sparse overstory of pinyon pine (*Pinus edulis*) and juniper (*Juniperus osteosperma*) between 1350 m and 1800 m. Dense pinyon-juniper stands with a sagebrush (*Artemisia tridentata*) understory dominate the vegetation between 1800 m and 2400 m. Ponderosa pine (*Pinus ponderosa*) and oakbrush (*Quercus gambelii*) are prominent above 2400 m where rocky, vertical-walled canyons with large areas of bare sandstone characterize the topography. Subalpine meadows with small stands of Engelmann spruce (*Picea engelmanii*), quaking aspen (*Populus tremuloides*), and white fir (*Abies concolor*) occur above 2700 m. River canyons transverse the area with associated vegetation consisting primarily of Fremont cottonwood (*Populus fremontii*) and willow (*Salix* spp.) (Ackerman 1982, Hemker 1982).

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The human population of about 800 is concentrated in the towns of Escalante and Boulder. Livestock grazing, timber harvesting, and energy exploration are the primary land uses in the area. Road density is about 25 km of road per 100 km^2 (Van Dyke et al. 1986). Hunting of cougars is prohibited on the study area.

METHODS

Capture and Monitoring Procedures

Cougars were tracked on horseback, treed with the aid of trained hounds, and immobilized with an intramuscular injection of ketamine hydrochloride and xylazine hydrochloride (Hemker et al. 1984). Each immobilized cougar was fitted with a collar containing a motion-sensitive radio transmitter (Telonics, Inc., Mesa, Arizona). Radio-collared cougars were monitored with portable radio telemetry equipment on the ground and from the air. All radiolocations were assigned UTM coordinates and recorded to the nearest 100 m. An attempt was made to locate all radio-collared cougars a minimum of once each week.

The Boulder-Escalante study area, including areas occupied by collared cougars, was searched periodically for sign of new cougars (e.g., tracks, scats, scratches). When detected, uncollared cougars taking up residence and transients were captured and radio-collared.

Road Track Surveys

Cougar density was measured as both the number of known cougars per km^2 in the survey area and the number of home ranges of independent cougars overlapping the survey road. We conducted both systematic (Fitzhugh and Smallwood 1988) and random-systematic (Van Dyke et al. 1986) road track surveys. Only dirt roads were surveyed.

For the systematic survey the study area was divided into three survey areas spatially and behaviorally (home range boundaries) isolated from the others. One 11.3-km section of road was chosen in each area; roads were similar in elevation change, habitat type, and condition (substrate, surface condition). Survey areas differed in density (independent adult cougars per km^2) and the number of home ranges that intersected road sections: 2–3 in the first, 4–5 in the second, and 6–7 in the third.

Roads were surveyed from a pickup truck at 8–12 kph. Each road including both shoulders was dragged with a conifer tree pulled from the rear of the truck. The following day both sides of the road were searched for cougar track sets by driving on one side and returning on the other. A track set was defined as a continuous set of tracks created by one cougar on a single occasion. Three to 10 days later each road was again surveyed and dragged. We felt that after 3 days the effect of dragging would be minimal, and movements of cougars in the area (Hemker et al. 1984) suggested this interval would be sufficient to provide independent sampling periods. Dust ratings, determined from imprint characteristics of the observer's shoe (Van Dyke et al. 1986), were conducted every km before and after dragging to quantify road surface condition. At each stop the observer took 10 steps, 5 on each shoulder; then each impression was given a point value from 1 to 4. Simple regression analyses were used to examine the relationship between track sets per km surveyed and both measures of density. Track sets per km surveyed were considered the independent variable because only these data would be available to the manager.

The random-systematic road track survey involved dividing the study area into four survey areas. Again, the four areas were spatially and behaviorally isolated from each other. Two survey areas had 2–4 cougar home ranges overlapping roads and two had 5–7. Each area had a different density of cougars (0.017, 0.032, 0.042, 0.057 cougars/km^2). A 16-km stretch of road was randomly selected in each area, and the first area to be surveyed was randomly chosen. Surveys were run as described for systematic surveys except that an all-terrain vehicle was used and only one shoulder of the road was dragged. Once all four areas had been surveyed, we returned to the first area, randomly selected different 16-km survey routes for each area and began the sequence again. Surveyed roads were not eligible for resampling until all dirt roads within an area had been sampled once. For analyses, each 16-km section of road was divided into segments varying in length from 1 to 10 km depending on the number of home

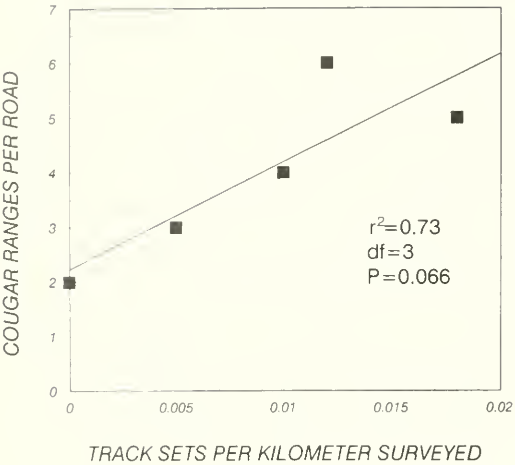

Fig. 1. Relationship between cougar track sets per kilometer and cougars with home ranges overlapping the survey road on the Boulder-Escalante study area, Utah, 1988.

ranges overlapping the segment. Each segment then had a home range overlap value (2–7) and was assigned one of the four density values.

We examined the relationship between track sets found per km surveyed and the two measures of density with simple regression analysis. Road segments with the same home range overlap values were combined to obtain km surveyed, as were road segments representing the same densities. Data points entered into the regression equations were the sum of tracks found in each of the six home range overlap or four density categories divided by the sum of km surveyed in the respective categories.

We evaluated whether dragging would improve survey roads with a simple regression of pre-drag dust ratings against post-drag ratings. Data from both road track surveys were combined to increase sample size, and regression slopes were tested against 1. The number of track sets found on dragged and undragged roads was also compared by dividing the total number of track sets in each by the total km searched in each.

Multiple regression analysis was used to examine the effect of rainfall and traffic on one-day, post-drag dust ratings. Pre-drag dust ratings, rainfall, and traffic were the independent variables considered. We used two indicator variables to code the three levels of rainfall and two to code the three levels of traffic. The three road surface categories related to increasing rainfall intensity were: unchanged, dimpled (individual raindrop impressions distinct), and deformed. Traffic categories were: no traffic, traffic on one-half the length of the road, and traffic on more than one-half the length.

RESULTS

The systematic road track surveys were conducted May–June 1988. During this period 407 km of road was surveyed and two track sets were found. One-hundred thirty-five km (12 surveys) of road was surveyed in an area where 2–3 ranges overlapped the survey road, 146 km (13 surveys) where 4–5 ranges overlapped, and 126 km (11 surveys) where 6–7 ranges overlapped the survey road. Unequal survey numbers resulted from weather or equipment problems precluding surveys being run. Each road (11.3 km) was surveyed in three hours, with two areas being surveyed the first day and the third the next day. The two track sets were found on a road overlapped by 4–5 cougar home ranges. Because of the small number of track sets found, these results were not regressed against either measure of density.

Random-systematic road track surveys were run in July and August 1988. During this period 684 km was surveyed and seven cougar track sets were found. Three hundred fifty km (37 road segments) was located in an area of low-home-range/road overlap and 334 km (42 road segments) in high. The number of km searched per day was 16.

We identified no relationship between density, as measured in cougars per km^2, and track finding frequency (r^2 = .00, P = .886, n = 4). However, the relationship ($Y = 2.23 + 197X$, r^2 = .73, P = .066, ROOT MSE = 1, n = 5) between number of cougars known to have home ranges overlapping the road and track-finding frequency was positive (Fig. 1). The data point associated with the home range overlap value of 7 was dropped because <20 km of road was surveyed. Results from both one-day periods and three or more days were combined for these analyses.

Because of the small number of track sets found, we did not statistically evaluate the relationship between track-finding frequency and dust rating categories or dragged and undragged roads. We found a positive relationship between post-drag dust ratings (Y) and pre-drag ratings after one ($X1$) and three or more ($X2$) days (r^2 = .54, $Y = 6.05 + 0.875X1$, P < .001, ROOT MSE = 10.4, n = 43) (r^2 = .34, $Y = 3.14 + 0.707X2$, P < .01, ROOT MSE = 4.6, n = 20). However, we failed to reject the null hypothesis (slope = 1) in both cases, indicating that our method of road dragging did little to improve tracking medium or that dust ratings were not sensitive enough to detect changes in the tracking medium. Data associated with heavy rainfall were omitted from these analyses. Multiple regression analysis (one day) relating post-drag dust ratings to pre-drag dust ratings, rainfall, and traffic yielded a three-variable model that contained only pre-drag dust ratings (X1) and rainfall (X2, X3) as the independent variables ($r^2 = .67$, $Y = 7.65 + 0.838X1 + 0.76X2 - 5.65X3$, $P < .000[X1]$, $P < .583[X2]$, $P < .001[X3]$, ROOT MSE = 9, $n = 43$). Moderate rainfall had little effect on post-drag dust ratings. However, heavy rainfall resulting in road surface deformity had a deleterious effect on post-drag dust ratings. The effect of traffic on post-drag dust ratings was not significant ($P > .05$).

DISCUSSION

The utility of road track surveys for monitoring cougar abundance is limited by the generally poor relationship between cougar density and track-finding frequency. Both our results ($r^2 = .00$), although based on a small sample, and those of Van Dyke et al. (1986) ($r^2 = .18$) indicate a weak relationship between cougar density and track-finding frequency. The strongest significant relationship found by Van Dyke et al. ($r^2 = .61$) resulted from a multiple regression model with track-finding frequency the dependent variable and female density, good tracking conditions, and proximity of cougars to survey road the independent variables. As the authors noted, however, a biologist would seldom have knowledge of cougar distribution in regard to survey roads.

The poor relationship documented between track-finding frequency and cougar density appears the result of sampling problems, largely beyond the control of the biologist. Cougars are rarely uniformly distributed (Hemker et al. 1984), and available roads, the sampling strata, are seldom abundant enough or optimally located to sample from a nonuniform distribution. Available roads, for example, could fail to intercept any cougar home ranges or could be found only in the areas occupied by cougars. In both scenarios, the index (tracks found) could easily prove to be a poor measure of change in cougar numbers over time in an area. Likewise, because of the potential importance of road location in determining number of tracks found, use of index values to compare cougar density between areas in tenuous. The probability of existing road networks in two areas sampling similarly from the two populations seems small. Use of track surveys to document cougar presence is feasible, but again, the approach ultimately relies on roads intersecting a cougar home range.

Ideally, roads with suitable tracking surface should be abundant, as in parts of the Northwest where logging is common, and located so that the home range of each cougar would be intercepted. Even in an ideal situation, however, the index may prove sensitive only to relatively large changes in cougar population size. Twenty-seven percent of the variance in number of tracks found was unexplained by number of cougar home ranges overlapping survey roads.

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LEAF AREA RATIOS FOR SELECTED RANGELAND PLANT SPECIES

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ABSTRACT.—Leaf area estimates are required by hydrologic, erosion, and growth/yield simulation models and are important to the understanding of transpiration, interception, CO_2 fixation, and the energy balance for native plant communities. Leaf biomass (g) to leaf area (mm^2) linear regression relationships were evaluated for 15 perennial grasses, 12 shrubs, and 1 tree. The slope coefficient (β_0) of the linear regression equation is a ratio of leaf area to leaf biomass and is defined as the leaf area ratio [LAR = one-sided leaf area (mm^2)/oven-dry leaf weight (g)]. LAR represents β_0 in each regression equation, where $Y = \beta_0(X)$. Linear regression relationships for leaf area were computed ($r^2 = .84-.98$) for all 28 native range species after full leaf extension. Within-plant estimates of leaf area for mesquite (*Prosopis glandulosa* Torr. var. *glandulosa* [Torr.] Cockll.) or lime prickly ash (*Zanthoxylum fagara* [L.] Sarg.) were not significantly different ($P \leq .05$). LARs for three of the shrubs and the tree were established at four different phenological stages. There were no significant differences ($P \leq .05$) in LARs for lime prickly ash, mesquite, and Texas persimmon (*Diospyros texana* Scheele) after full leaf extension during the growing season. The LAR relationship for Texas persimmon changed significantly after full leaf extension. LAR relationships for Texas colubrina (*Colubrina texensis* [T. & G.] Gray) changed in response to water stress.

Key words: leaf area index, drought response, leaf biomass.

Eighty percent of the world's rangeland is classified as arid or semiarid (Branson et al. 1981), i.e., precipitation is less than evapotranspiration. Under these conditions water availability is the most important environmental factor controlling plant production and survival (Brown 1977). Evapotranspiration (ET) is the major component of the water balance and is estimated to account for 96% of annual precipitation for rangeland ecosystems (Branson et al. 1981, Carlson et al. 1990), with surface runoff accounting for most of the remaining 4% (Gifford 1975, Lauenroth and Sims 1976, Carlson et al. 1990).

Evapotranspiration has been measured for selected rangeland plant communities with lysimeters and the Bowen ratio method (Wight 1971, Hanson 1976, Gay and Fritschen 1979, Carlson et al. 1990). Estimates of ET for unmeasured rangeland plant communities are usually simulated from hydrologic models (Lane et al. 1984, Wight 1986). For hydrologic simulation models to be biologically meaningful, improved methods of simulating evapotranspiration from rangeland plant communities are needed. Two different approaches are currently being used. One approach is to use a crop coefficient (Kc) (Wight 1986). Kc is defined as the ratio of actual evapotranspiration to evapotranspiration when water is nonlimiting. This empirical method is extremely difficult to parameterize for rangelands because water is often limiting and estimates of transpiration are confounded by soil water evaporation (Wight and Hansen 1990). Thus, Wight and Hansen (1990) reported that Kc values were not transferable across range sites. The second method is based on leaf area index (LAI) (Ritchie 1972). LAI is defined as the foliage area per unit land area (Watson 1947). The LAI method is more process-based than the Kc approach and has been successfully used in several rangeland hydrologic, erosion, and growth/yield simulation models (Wight and Skiles 1987, Lane and Nearing 1989, Arnold et al. 1990).

A limitation in using natural resource models, like the Water Erosion Prediction Project (WEPP) (Lane and Nearing 1989), is in developing LAI coefficients for rangeland plants. LAI is difficult to measure because of the drought-deciduous nature of certain shrubs, in which several cycles of leaf initiation and defoliation occur within a single growing season (Ganskopp and Miller 1986) and seasonal

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TABLE 1. Description of study sites, range sites, and soil series of species evaluated for leaf area to leaf biomass relationships.

Location	Range site	Mean PPT (mm)	Frost-free period (days)	Soil series	Soil family
Tombstone, AZ	Limey upland	356	239	Stronghold	Coarse-loamy, mixed thermic, Ustollic Calciorthid
Meeker, CO	Clayey slopes	200	180	Degater	Clay, montmorillonitic, mesic, Typic Camborthid
Sidney, MT	Silty	300	130	Vida	Fine-loamy, mixed, Typic Argboroll
Chickasha, OK	Loamy prairie	927	200	Grant	Fine-silty, mixed, Udic Arginstoll
Chickasha, OK	Eroded prairie	927	200	Eroded Grant	Fine-silty, mixed, Udic Arginstoll
Ft. Supply, OK	Dune	597	200	Pratt	Sandy, mixed, thermic, Psammentic Haplustalf
Woodward, OK	Shallow prairie	584	200	Quinlan	Loamy, mixed, thermic, shallow Typic Ustochrept
Alice, TX	Fine sandy loam	710	280	Miguel	Fine, mixed, hyperthermic, Udic Paleustalf
Sonora, TX	Shallow	609	240	Purves	Fine-loamy, mixed, thermic, Typic Calciustoll

changes in leaf size, shape, and/or thickness result from water, nutrient, and chemical stresses (Cutler et al. 1977, Curtis and Luchli 1987). Foliar surface area of irregular-shaped tree leaves has been estimated by coating the leaves with a monolayer of glass beads and measuring displacement (Thompson and Leyton 1971) and by estimating from photographs (Miller and Schultz 1987). Miller et al. (1987) estimated total surface area of juniper foliage from projected leaf area determined from a leaf area meter. Miller et al. suggested this method underestimated leaf area by 10% due to leaf overlap. Cregg (1992) reported that leaf area could be satisfactorily estimated from leaf weight or volume for *Juniperus virginiana* and *J. scopulorum*. However, leaf area relationships differed by crown position and seed source. Sapwood area, stem diameter, tree height, canopy area, and canopy volume have been correlated to total shrub biomass and leaf biomass (Ludwig et al. 1975, Brown 1976, Rittenhouse and Sneva 1977, Whisenant and Burzlaff 1978, Ganskopp and Miller 1986, Hughes et al. 1987). In contrast, only a few studies have estimated leaf area and LAI for rangeland plant communities (Goff 1985, Ganskopp and Miller 1986, and Ansley et al. 1992).

An effective method is needed to improve LAI estimates for natural resource models. One potential approach for improving LAI estimates is with the leaf area ratio (LAR) method (Radford 1967). LAR is defined as the ratio of leaf area per unit weight of plant material. The slope coefficient (β_0) of the linear regression equation is a ratio of leaf area to leaf biomass and is defined as the leaf area ratio [LAR = one-sided leaf area (mm^2)/oven-dry leaf weight (g)]. LAR represents β_0 in each regression equation, where $Y = \beta_0(X)$. LAI can be calculated as the product of LAR and live biomass per unit area. The objective of this study was to determine LARs for selected rangeland species.

MATERIALS AND METHODS

The study area included nine range sites in five states and was part of the USDA Water Erosion Prediction Project (WEPP) (Table 1). The dominant plants on each range site were evaluated. LARs for 15 grasses, 12 shrubs, and 1 tree were developed (Table 2). Selected rangeland species were sampled once during the summer of 1987 near Tombstone, Arizona; and in 1987 near Meeker, Colorado; Sidney, Montana; Chickasha, Ft. Supply, and Woodward, Oklahoma; and Sonora, Texas, sites. Seasonal fluctuations in LAR for three shrubs and one tree were evaluated near Alice, Texas, in 1985 and 1986.

For leaf area determination grass leaf biomass from 10 randomly located 0.25-m^2 quadrats was

TABLE 2. Location of study sites, sample dates, height class, number of samples, and species evaluated for leaf area to leaf biomass relationships.

		Height class (m)					Species	
Location	Sample date	0–1	1–2	2–3	3–4	>4	Common name	Scientific name
Tombstone, AZ	Aug. 1983	6	6				Little leaf sumac	*Rhus microphylla* Engelm.
	Aug. 1983	7	8				Tarbush	*Flourensia cernua* DC.
	Aug. 1983	8					Broom snakeweed	*Gutierrezia sarothrae* (Pursh) Britt. & Rusby.
	Aug. 1983	10	10				Creosotebush	*Larrea tridentata* (DC.) Coville
	Aug. 1983	15					Desert zinnia	*Zinnia pumila* Gray
	Aug. 1983	15					Mariola	*Parthenium incanum* H.B.K.
Meeker, CO	June 1987	10					Shadscale saltbush	*Atriplex confertifolia* (Torr. & Frem.) Wats.
	June 1987	10					Wyoming big sagebrush	*Artemisia tridentata* subsp. *wyomingensis* Beetle & Young
Sidney, MT	July 1987	10					Needle-and-thread	*Stipa comata* Trin. & Rupr.
	July 1987	10					Western wheatgrass	*Agropyron smithii* Rydb.
Chickasha, OK	June 1987	10					Indiangrass	*Sorghastrum nutans* (L.) Nash
	June 1987	10					Big bluestem	*Andropogon gerardii* Vitman
	June 1987	10					Little bluestem	*Schizachyrium scoparium* (Michx.) Nash
Chickasha, OK	June 1987	10					Buffalograss	*Buchloe dactyloides* (Nutt.) Engelm.
	June 1987	10					Scribners dichanthelium	*Dichanthelium oligosanthes* (Schult.) Guild var. *scribnerianum* (Nash) Gould
	June 1987	10					Sand paspalum	*Paspalum setaceum* Michx. var. *stramineum* (Nash) D. Banks
Ft. Supply, OK	June 1987	10					Sand sagebrush	*Artemisia filifolia* Torr.
	June 1987	10					Tall dropseed	*Sporobolus asper* (Michx.) Kunth
	June 1987	10					Sand lovegrass	*Erogrostis trichodes* (Nutt.) Wood
Woodward, OK	June 1987	10					Hairy grama	*Bouteloua hirsuta* Lag.
	June 1987	10					Sideoats grama	*Bouteloua curtipendula* (Michx.) Torr.
Alice, TX	May 1985	4	4	4	4	4	Honey mesquite	*Prosopis glandulosa* Torr. var. *glandulosa* (Torr.) Cockll.
	Aug. 1985	2	2	2	2	2		
	Nov. 1985	2	2	2	2	2		
	Jan. 1986	NA[a]						
	Apr. 1986	2	2	2	2	2		
	May 1985	5	5	5	5	5	Lime prickly ash	*Zanthoxylum fagara* (L.) Sarg.
	Aug. 1985	3	3	3	3			
	Nov. 1985	3	3	3	3			
	Jan. 1986	3	3	3	3			
	Apr. 1986	3	3	3	3			
	May 1985	5	5				Texas colubrina	*Colubrina texensis* (T. & G.) Gray
	Aug. 1985	5	5					
	Nov. 1985	5	5					
	Jan. 1986	5	5					
	Apr. 1986	5	5					
	May 1985	5	5				Texas persimmon	*Diospyros texana* Scheele
	Aug. 1985	5	5					
	Nov. 1985	5	5					
	Jan. 1986	NA						
	Apr. 1986	5	5					
Sonora, TX	June 1987	10					White tridens	*Tridens albescens* (Vasey) Woot. & Standl.
	June 1987	10					Curly mesquite	*Hilaria belangeria* (Steud.) Nash
	June 1987	10					Texas wintergrass	*Stipa leucotricha* Trin. & Rupr.

[a] No sample collected for deciduous shrubs and trees

TABLE 3. Mean and standard error of leaf biomass and leaf area, and linear regression[a] model slope coefficients (LAR[b]) relating leaf area to leaf biomass for selected rangeland grasses and shrubs sampled after full leaf extension.

Species	Leaf biomass (g)	SE	Leaf area (mm^2)	SE	LAR (mm^2g^{-1})	r^2
GRASSES						
Needle-and-thread	3.6	0.80	3,580	900	1,040	.98
Western wheatgrass	2.0	0.33	5,760	902	2,910	.98
Indiangrass	8.5	1.56	82,670	1,350	9,440	.96
Little bluestem	2.7	0.38	28,030	4,710	10,780	.98
Big bluestem	1.3	0.45	11,290	2,213	12,970	.86
Buffalo grass	1.5	0.22	6,820	1,091	5,680	.97
Scribners dichanthelium	1.3	0.21	15,300	2,601	16,110	.96
Sand paspalum	1.5	0.23	7,580	1,136	6,890	.95
Tall dropseed	0.9	0.15	8,500	1,334	9,390	.99
Sand lovegrass	0.8	0.12	8,650	1,383	11,380	.98
Hairy grama	0.7	0.13	4,360	769	5,890	.99
Sideoats grama	0.6	0.22	5,240	2,836	10,210	.98
White tridens	0.7	0.16	3,980	1,007	5,830	.98
Texas wintergrass	1.2	0.24	8,320	1,361	6,720	.95
Curly mesquite	0.8	0.15	5,270	925	6,620	.99
SHRUBS						
Desert zinnia	1.6	0.10	9,440	580	5,700	.89
Mariola	3.5	0.40	19,410	1,280	5,690	.84
Broom snakeweed	3.7	0.51	11,160	920	2,700	.96
Little leaf sumac	3.9	0.71	22,050	331	4,700	.91
Tarbush	3.7	1.00	23,360	203	6,100	.97
Creosotebush	3.0	0.19	16,790	910	3,660	.86
Sand sagebrush	3.2	0.58	5,950	1,257	2,010	.98
Shadscale saltbush	3.9	0.81	10,530	2,047	2,640	.98
Wyoming big sagebrush	5.3	0.83	18,220	2,715	3,340	.97

[a] All area weight regressions were significant at $P \leq .05$

[b] Leaf area ratio (LAR) represents β_0 in each regression (where $Y = \beta_0 X$)

used. Grass biomass in each quadrat was clipped to a 20-mm stubble height and separated by species into live or dead leaves. Live leaves were placed in plastic bags on ice for later determination of leaf area. The leaves were flattened and placed between clear plastic sheets and then processed through a leaf area meter. Leaf area was determined with a Li-Cor 3000[3] leaf area meter to the nearest 1 mm^2. The samples were then oven-dried at 60 C for three days and dry mass determined.

To ensure that samples of shrubs and trees represented the full range of size of plants present, a stratified random sampling procedure was used. Height classes of 1 m were arbitrarily chosen and plants were selected randomly from each class. As a result, total number of plants sampled varied among species depending upon the range of plant heights (Table 2).

An open-ended cube (250 mm on a side) was used to sample shrub and tree leaf biomass. The sample cube was placed in an area considered representative of the entire canopy, and the leaves within the area were removed by hand. LARs were determined in the same manner as for grasses.

Within-plant variability of LARs was evaluated for four mesquite trees and four lime prickly ash shrubs in May 1985 near Alice, Texas. Fifteen sample cubes were randomly located and sampled from each of the four mesquite trees. For the lime prickly ash shrubs 12 sample cubes were harvested from each of the four shrubs. LAR was determined in the same manner as previously described. A one-way analysis of variance was used to test for differences ($P \leq .05$) among the slopes of the regression equations within plant canopy by species (Steel and Torrie 1980). Within-plant LARs were not significantly different for lime prickly ash and mesquite in May 1985. Based on these relationships, one sample per plant was utilized during the remainder of the study.

Three shrubs, lime prickly ash, Texas persimmon, and Texas colubrina, and one tree,

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[3] The mention of trade or firm names in this publication [illegible] and does not imply endorsement by the U.S. Department of Agriculture of any product or service.

TABLE 4. Mean and standard error of leaf biomass and leaf area, and linear regression[a] model slope coefficients (LAR[b]) relating leaf area to leaf biomass for selected rangeland shrubs and tree on a fine sandy loam range site near Alice, Texas.

Species	Date	Leaf biomass (g)	SE	Leaf area (mm^2)	SE	LAR ($mm^2 g^{-1}$)	r^2
Lime prickly ash	May 1985	4.7	0.73	45,180	1,450	8,760 a[c]	.99
	Aug. 1985	4.2	0.63	40,330	1,530	8,730 a	.98
	Nov. 1985	5.6	0.89	43,360	1,460	8,670 a	.98
	Jan. 1985	4.9	0.76	44,310	1,450	8,870 a	.98
	Apr. 1986	5.3	0.65	52,730	1,580	8,690 a	.98
Mesquite	May 1985	6.5	0.87	57,830	1,610	8,990 a	.98
	Aug. 1985	5.7	0.64	56,040	1,470	8,780 a	.98
	Nov. 1985	5.5	0.70	48,460	1,410	8,630 a	.98
	Jan. 1985	NA[d]					
	Apr. 1986	6.4	0.81	59,100	1,470	9,290 a	.98
Texas persimmon	May 1985	4.6	0.64	49,960	1,940	10,590 b	.96
	Aug. 1985	4.1	0.65	41,670	1,780	10,360 b	.98
	Nov. 1985	4.8	0.59	51,060	1,790	10,130 b	.98
	Jan. 1986	4.6	0.68	44,720	1,900	10,020 b	.98
	Apr. 1986	4.7	0.69	64,150	2,070	12,660 a	.97
Texas colubrina	May 1985	4.9	0.78	55,070	2,020	10,310 b	.98
	Aug. 1985	5.2	0.89	57,010	1,720	10,110 b	.98
	Nov. 1985	3.8	0.65	55,380	2,090	13,360 a	.98
	Jan. 1986	NA					
	Apr. 1986	4.1	0.71	41,760	1,880	10,230 b	.98

[a] All area: weight regressions were significant at $P < .05$

[b] Leaf area ratio (LAR) represents β_0 in each regression, where $Y = \beta_0 X$)

[c] Parameters in the columns by species sharing a common letter are not significantly different ($P \leq .05$) based on homogeneity of slope test

[d] No sample was collected for deciduous shrubs

honey mesquite, were selected for evaluation of seasonal fluctuation in LAR. Honey mesquite, Texas persimmon, and Texas colubrina are drought-deciduous while lime prickly ash is an evergreen. Sample dates were selected to correspond to the phenological stages of (1) maximum leaf area, (2) peak drought defoliation, (3) autumn, just prior to winter leaf fall and dormancy, and (4) after winter leaf fall for the deciduous shrub.

The Statistical Analysis System (SAS 1982) was utilized to evaluate linear regression relationships, $Y = \beta_0 + \beta_1(X)$, between leaf biomass and leaf area. Where Y is estimated leaf area (mm^2), β_0 is the intercept, β_1 is the slope (LAR coefficient as defined by Radford 1967 in $mm^2 g^{-1}$), and X is leaf biomass (g). The intercept was tested to determine if it was significantly different ($P \leq .05$) from zero. The intercept was not significantly different from zero for all species. Therefore, the data were reanalyzed and presented using a linear regression model, $Y = \beta_0(X)$, similar to that reported by Coombs et al. (1987) and Ansley et al. (1992) for estimating LAR. All statistical tests were judged significant at $P \leq .05$ unless otherwise stated. A homogeneity of slope test was used to test for differences among the slopes of the regression equations (LAR) between sample periods within species (Steel and Torrie 1980).

RESULTS AND DISCUSSION

Leaf area of graminoids was highly correlated with leaf biomass for all species within sample dates (Table 3). The LAR for perennial grass leaf area ranged from 2910 to 16,110 $mm^2 g^{-1}$. The LAR for shrubs and trees ranged from 2010 to 13,360 $mm^2 g^{-1}$. Goff (1985) also reported significant linear regression relationships ($r^2 = .83–.97$) for LAR for 11 native grass species in southern Arizona. Goff reported that the linear regression coefficients for stem area to stem biomass (SAR) ranged from 32 to 73% of the LAR and the mean SAR was 44% of the mean LAR.

There was no significant seasonal variation in LAR for lime prickly ash and mesquite (Table 4). Although there was no significant seasonal difference between mesquite LAR relationships, a gradual decrease in the LAR from May through November was apparent in 1985. Furthermore, the LAR was larger in April 1986, though it was not significantly different from 1985 sampling dates. Mooney et al. (1977) found that the specific leaf density (mg mm^{-2}) of mesquite leaves increased over the growing season. The density ranged from 0.0004 mg mm^{-2} in the spring to 0.017 mg mm^{-2} in the fall. This corresponds with a leaf area change of 5880 to 25,000 mm^2 g^{-1}.

Ansley et al. (1992), working in north central Texas, reported that LAR of mesquite ranged from 9916 to 5944 mm^2 g^{-1}. Mesquite LAR declined from May through August 1987, but stabilized from August through September following substantial precipitation. In 1988 precipitation was substantially less than in 1987, and the mean LAR was significantly lower than in 1987. LAR followed the same pattern in 1988, declining from a high of 6877 in the spring to a low of 4996 mm^2 g^{-1} in October. Ansley et al. (1992) speculated that the decline in LAR was caused by cell-wall thickening in response to drying conditions, based on the work of Kramer and Kozlowski (1979).

The similarity in LAR across sampling dates from this study may be partially explained in that sampling was not initiated until all leaves were fully expanded for approximately four weeks. In addition, April, May, June, and September precipitation was significantly above the long-term average precipitation and no noticeable water stress was apparent in the trees sampled. Nilsen et al. (1986) indicated that relative leaf area of phreatophytic mesquite (*P. glandulosa* var. *torreyana*) in the Sonoran desert of southern California remained nearly constant from May through November. Maximum leaf area was maintained throughout the hottest and driest months of the year via access of deep stored soil water by taproots. When water availability to the normally phreatophytic mesquite was reduced, total leaf area was reduced (Nilsen, Virginia, and Jarrell 1986). We hypothesized that mesquite leaves reach a stable weight at maturity and the lack of water stress during the growing season prevents the changes in leaf weight to leaf area reported by Ansley et al. (1992). Changes in leaf weight as a result of translocation of sugars, starches, other compounds, and insect damage could not be detected or separated from cell-wall thickening from water stress within the precision of sampling in our study.

Texas persimmon LAR in April 1986 was significantly greater than for sampling dates in 1985. Meyer (1974) reported that Texas persimmon produces two types of leaves: a large leaf in the center of the canopy and a smaller leaf around the perimeter of the plant. The leaves are initially light green in color and become glabrous after elongation ceases. As the leaf matures, the xylem and bundle fibers become increasingly lignified and the leaf turns dark green, with the underside becoming densely covered with trichomes. Leaf modification is complete by early July. The lower LAR of Texas persimmon leaves in 1986 was attributed to the leaves not being fully elongated, with incomplete development of trichomes and lignification.

LAR relationships for Texas colubrina varied seasonally. LAR was similar during the early growing seasons in May 1985 and April 1986, and in August 1985. In November the LAR was 33% greater than during other sample dates (Table 4). Basal leaves of Texas colubrina are approximately 10 times larger than the outer canopy leaves. In response to an extended dry period in July and August, Texas colubrina dropped 95% of its leaves. The only leaves retained during this dry period were the large basal leaves in the center of the shrub. The significant difference in LAR between the sample dates was attributed to the different proportion of leaf types and not the change in specific weight of the leaves.

Ganskopp and Miller (1986) reported similar significant seasonal changes in LAR for Wyoming big sagebrush. They speculated that the greatest proportion of seasonal variation was due not to the development or alterations in starch and sugar accumulations but rather to changes in the proportion of larger persistent leaves to smaller ephemeral leaves.

Shrub leaf biomass to leaf area was highly correlated for the nine other shrubs sampled (Table 3). The LAR for shrub leaf area ranged from 2010 to 6100 mm^2 g^{-1}. Other researchers have also reported satisfactory results in relating leaf biomass to leaf area (Schilesinger and Chabot 1977, Kaufmann et al. 1982, Ganskopp and Miller 1986) within sample date. Based on the seasonal variability in LAR for Texas persimmon and Texas colubrina in this study and the findings of Ganskopp and Miller (1986) in eastern Oregon for Wyoming big sagebrush, we can state that seasonal variability in these and other drought-deciduous shrubs is an important source of variation that needs to be accounted for when simulating LAI over the entire growing season.

CONCLUSION

For the species sampled, leaf biomass is a reliable estimator of leaf area. However, for some shrub species, seasonal differences in development and shedding of different types of leaves and leaf morphological development can produce significant temporal fluctuations in LAR. Caldwell et al. (1981) reported that for semiarid bunchgrasses, leaf blades of regrowing tillers had greater photosynthetic capacity than blades on unclipped plants. This resulted in greater carbon gain for clipped plants and an increased photosynthesis/transpiration ratio. Nowak and Caldwell (1984) reported that the photosynthetic rate for both clipped and unclipped plants decreased with age of the leaves. Current rangeland hydrologic simulation models do not account for changes in LAR or evapotranspiration rates as a function of age of the leaf, proportion of leaf type, or compensatory photosynthesis rate increases following defoliation due to grazing. Models currently utilize a fixed coefficient for calculating LAI. If significant advances in modeling evapotranspiration on rangelands are to be made, improvements in the relationships used to simulate evapotranspiration that incorporate these processes will be needed. The LAR method of calculating LAI evaluated in this study provides a fast, reliable method of estimating LAI necessary to parameterize these hydrologic simulation models. To account for the seasonal differences in LAR for Texas persimmon and Texas colubrina, a weighted average based on season of year is recommended for parameterizing the WEPP model. For plants like mesquite and lime prickly ash, one LAR value can be used in non-drought years. For years with significant dry periods, a decrease in LAR of 10–40% may need to be accounted for with non-phreatophytic mesquite, as indicated by this work and that of Ansley et al. (1992).

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ECOLOGY AND MANAGEMENT OF MEDUSAHEAD (*TAENIATHERUM CAPUT-MEDUSAE* SSP. *ASPERUM* [SIMK.] MELDERIS)

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ABSTRACT.—Medusahead is another in the extensive list of annual herbaceous species to invade the temperate desert rangelands of the Great Basin. Medusahead is not preferred by large herbivores and apparently is not preferred by granivores. Herbage of this annual grass enhances ignition and spread of wildfires. Medusahead is highly competitive with the seedlings of native species and is probably the greatest threat to the biodiversity of the natural vegetation that has yet been accidentally introduced into the Great Basin. Despite the obvious biological disruptions that are associated with medusahead invasion, the species offers a wealth of opportunities for students to examine the mechanism by which this species is so successful. Students of evolution, plant physiology, and ecology may find this species to be an excellent model for colonization.

Key words: medusahead, Taeniatherum caput-medusae, *annual grass, colonizing species, wildfires, grazing.*

In the management of natural resources there are certain problems that by their persistence, magnitude of ecological disruption, and economic impact refuse to dissipate as a result of being ignored and neglected. Unfortunately for range management, medusahead (*Taeniatherum caput-medusae* [L.] Nevski) is that type of problem. During the 1950s medusahead was considered among the most pressing problems on the rangelands of California, Idaho, and Oregon. A great deal of research effort was devoted to solving the medusahead problem. Valuable information was learned about the ecophysiology and synecology of medusahead. Control methods were developed using herbicides. The fatal link in integrated programs for the suppression of medusahead populations proved to be artificial revegetation technologies after medusahead was controlled. The nature of the sites infested had more to do with this failure than the weed itself, especially in the Intermountain area. The recent discovery of medusahead in northern Utah has renewed interest in suppressing this rangeland weed.

My purpose in this review is to refresh our collective memories about medusahead ecology and management.

TAXONOMY

As is often the case with an introduced species, there has been confusion about the correct scientific taxon for medusahead. The first description of medusahead in a North American flora used the taxon *Elymus caput-medusae* L. (Howell 1903). There is apparent agreement that medusahead is a member of the tribe Triticeae of the grass family. There is also apparent agreement among morphologists and cytogeneticists that medusahead does not fit in the genus *Elymus*. Various authors have placed medusahead in *Hordeum* or *Hordelymus*. Nevski (1934) proposed that medusahead was truly a different genus and published the name *Taeniatherum*. Jack Major of the University of California suggested in 1960 that material introduced to the United States was *Taeniatherum asperum* (Major et al. 1960). Based on the European and Russian literature, Major reported that *Taeniatherum* contained three geographic and morphologically distinct taxa, *T. caput-medusae*, *T. asperum*, and *T. crinitum*. These three species are found in the Mediterranean region and extend eastward into central Asia. After examining the European material, growing in place, Major decided the United States introduction was *T. asperum*.

The Danish scientist Signe Frederiksen revised the genus in 1986. He kept the same three taxa, but reduced them to subspecies of *Taeniatherum caput-medusae*. Positive identification to the lowest level possible is absolutely essential for any proposed biological control program for medusahead. According to Frederiksen's revision, subspecies *crinitum* has a very strict spike. Subspecies *caput-medusae* has a large open spike with straight awns. The spike of subspecies *asperum* is intermediate with angled awns. Subspecies *asperum* is the only one of the three with pronounced barbs coated with silica on the awns. Apparently, the correct taxon for the medusahead of western North America is *Taeniatherum caput-medusae* ssp. *asperum* (Simk.) Melderis (Frederiksen 1986).

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Taeniatherum caput-medusae ssp. *caput-medusae* is mostly restricted to Portugal, Spain, southern France, Morocco, and Algeria. It has been collected outside this area in Europe and Asia, but Frederiksen considers it adventitious in these areas. Subspecies *crinitum* is found from Greece and Yugoslavia eastward into Asia. Subspecies *asperum* completely overlaps the distribution of the other two subspecies. All three subspecies integrate with each other. Apparently only the one subspecies occurs in North America. Does this indicate one or very limited introductions?

Medusahead is predominantly self-pollinated. Genetically the genus appears to stand alone in genomic relations within the Triticeae (Schooler 1966, Sakamoto 1973). Apparently *Taeniatherum* has a genome that is distinct, but faintly related to those of *Psathyrostachys*, *Dasypyrum*, *Eremopyrum*, or *Hordeum* (Frederiksen and Bothmer 1989).

HISTORY IN NORTH AMERICA

Medusahead was first collected in the United States near Roseburg, Oregon, on 24 June 1887 by Thomas Jefferson Howell (1903). It was next collected near Steptoe Butte in eastern Washington in 1901 by George Vasey (Piper and Beattie 1914), followed by a collection near Los Gatos, California, in 1908 by Charles Hitchcock (Jepson 1923). Medusahead certainly attracted the noted agrologist. McKell, Robinson, and Major (1962) commented on this strange initial distribution reaching 390 miles north and 450 miles south from the point of initial collection. Early herbarium specimens show a rapid spread to the south into California.

J. F. Pechanec made the first collection in Idaho in 1944 near Payette or about 180 miles south of Steptoe Butte (Sharp and Tisdale 1952). Fred Renner told Jack Major he had seen medusahead near Mountain Home, Idaho, as early as 1930, and Lee Sharp had reports from ranchers that the species occurred in Idaho as early as 1942. The medusahead infestation in Idaho increased to 30,000 acres by 1952. Min Hironaka estimated that 150,000 acres were infested by 1955, and the Bureau of Land Management estimated 700,000 acres were infested by 1959. At that rate of spread it appeared that all of Idaho would be infested by the end of the next decade. The spread of medusahead slowed and nearly continuous infestations remained confined to Gem, Payette, and Washington counties in southwestern Idaho. There were several spot infestations in surrounding counties (Hironaka and Tisdale 1958).

Medusahead spread south in California to Santa Barbara on the southern coast and Fresno County in the interior valleys. The rapid spread from southwestern Oregon through northern and central California occurred in annual-dominated grassland, oak (*Quercus*) woodland, and chaparral communities. These areas have a Mediterranean type climate with hot, dry summers and cool, moist falls, winters, and springs. Germination occurs in the fall and flowering and seed set in the spring.

In northeastern California, east of the Sierra Nevada–Cascade rim, medusahead invasion occurred at a much slower rate. In the Pitt River drainage, vegetation is an intergrade of Oregon white oak (*Quercus garryana*) woodlands, cismontane California species, western juniper (*Juniperus occidentalis*), ponderosa pine (*Pinus ponderosa*) woodlands, and sagebrush (*Artemisia*)/bunchgrass communities more typical of the Intermountain area.

Medusahead was discovered in the Great Basin at Verdi, Nevada, in the early 1960s. Isolated infestations were subsequently found along the eastern front of the Sierra Nevada in areas where range sheep bands used to concentrate while waiting for mountain summer pastures to be free of snow.

In northeastern California in the Great Basin during the early 1960s, there were two small infestations in city lots in Susanville and a small infestation at the old sheep-shearing site of Viewland along the railroad above Wendel, California. Another isolated infestation occurred at the mouth of Fandango Pass in Surprise Valley. By the early 1970s, medusahead was nearly continuous over about 60,000 acres of the Willow Creek–Tablelands northeast of Susanville. Currently, after four years of extreme drought, medusahead spot infestations occur over perhaps an additional million acres on the western margin of the Great Basin.

BIOLOGY OF MEDUSAHEAD

Medusahead, in some ways, is a rerun of cheatgrass (*Bromus tectorum*) invasion. Cheatgrass dominates secondary succession in a majority of sagebrush/bunchgrass communities in the Great Basin and provides a significant portion of the forage base for livestock grazing. However, there are highly significant differences in the ecology of the two grass species (Harris and Wilson 1970, Al-Dakheel 1986).

GERMINATION.—The caryopsis of medusahead is less than a millimeter wide with a very sharp callus and an elongated, non-geniculated awn. The medusahead caryopsis is covered with small barbs of silica. Vicious is the best description for this grass caryopsis. Bovey et al. (1961) determined that medusahead had a much higher ash content (over 10%) than other grass species and the ash was about 75% silica. Heavy deposition of silica occurs on the barbs of awns and the epidermis of leaves.

For the vast majority of collections of cheatgrass from the Intermountain area, seeds are ready to germinate when they are mature. No pregermination treatments are necessary (Young and Evans 1982). For collections from the Great Plains and perhaps the Columbia Basin, seeds may have a brief afterripening dormancy. In contrast, seeds of medusahead have a temperature-related afterripening, and germination will not occur except at cold incubation temperatures for about 90–120 days after maturity (Young et al. 1968). Nelson and Wilson (1969) found this dormancy was controlled by materials located in the awn.

The high silica content on the herbage of medusahead makes the litter very slow to decompose. Harris (1965) described the choking accumulations of medusahead litter that built up for several years. We evaluated the germination of seeds of various annual grass species in medusahead litter (Young et al. 1971a). Allelopathy was not suspected, but rather the physical holding of seeds out of contact with the surface of the seedbed. Medusahead seeds germinate very well without the callus end of the seeds touching a moisture-supplying substrate. In this situation, germination of medusahead seeds is controlled by the relative humidity within the litter and the incubation temperature, which of course influences the relative humidity. The needlelike, vitreous caryopses of medusahead appear hydrophobic rather than hygroscopic. Not only can medusahead seeds germinate under these conditions, but they can be dried until the primary root is dead; then, following remoistening, a new adventitious root will develop.

Raymond Evans and I demonstrated what a great modifying influence litter cover can be to the surface of seedbeds on temperate desert rangelands in terms of reducing extremes in temperature and conserving moisture (Evans and Young 1970, 1972). Caryopses of squirreltail (*Elymus hystrix*) are very similar in morphological appearance to those of medusahead. As I will discuss later, squirreltail seedlings are one of the few native species that can become established in undisturbed medusahead stands. Both *Taeniatherum* and *Elymus* are members of the tribe Triticeae, but they do not share the same genome.

Medusahead populations easily exceed 1000 plants per square foot, and they are phenotypically plastic enough that a population of 1 plant per square foot can exceed the seed production of 1000 plants per square foot (unpublished research, ARS, Reno, Nevada). Huge seed banks develop in medusahead communities in the litter and soil. Medusahead seed acquires a dormancy in the field similar to that of cheatgrass (see Young et al. 1969). These dormant seeds respond to enrichment of the seedbed with nitrate and gibberellin (Evans and Young 1975).

LIFE CYCLE.—Medusahead seeds can germinate in the fall, winter, or spring; and seedlings from all seasons can produce flowers and seeds early in the summer. The striking thing about the medusahead life cycle is that it matures from 2 to 4 weeks later than other annual grasses. All those famous botanists and range scientists who were out on the range discovering new infestations of medusahead were led to the populations by the bright green color when all other annuals in either cismontane California or the Great Basin were brown.

R. L. Piemeisel recognized the dominance of alien plant species in the secondary succession of disturbed sagebrush communities in the

Intermountain area (Piemeisel 1951). Working on the Snake River plains of Idaho during the 1930s, Piemeisel enumerated dominance from Russian thistle (*Salsola australis*) to tumble mustard (*Sisymbrium altissimum*) to cheatgrass. Continued disturbance tended to perpetuate cheatgrass dominance. According to Piemeisel, the annual species that germinates first, reaches maximum growth and maturity first, has the capacity to withstand crowding, and has high seed production is the one that will occupy and persist in seral sagebrush plant communities. Piemeisel always noted that no one species had a clear dominance on all these characteristics, but on balance cheatgrass was the clear winner.

Medusahead contradicts several of Piemeisel's criteria. Medusahead seeds are initially dormant with temperature-related afterripening requirements, while cheatgrass seeds have no such restraints. This works only for initial establishment because once seed banks are established with seeds with acquired dormancy, our research indicates that cheatgrass and medusahead seeds have equal chances of germination with the initial moisture event in the fall. Medusahead does take much longer to mature than cheatgrass and perhaps tumble mustard. Min Hironaka and his students have conducted a series of excellent experiments comparing the cumulative growth curves for roots and aerial structures of medusahead and other grasses (Hironaka 1961, Hironaka and Sindelar 1973, 1975). Dr. Hironaka concluded from these studies that the comparative growth phenology restricts medusahead to areas with surplus soil moisture after cheatgrass normally matures.

Soils

Raymond Evans noted in the 1950s when medusahead first invaded Glenn and Colusa counties in the northern Sacramento Valley of California that medusahead appeared to be restricted to clay-textured soils (personal communication). Mallory (1960) reported on this relationship at the 1960 meeting of the California section of the Society for Range Management. Burgess Kay made the chilling observation that after a couple of decades this relationship disappeared and medusahead occupied many sites with coarser-textured soils (personal communications).

In the Intermountain area, Maynard Fosberg of the University of Idaho reported that the medusahead infestations along the Columbia River in Washington, Idaho, and Oregon were restricted to clay-textured soils (Fosberg 1965). He suggested that the greater soil moisture-holding capacity of these soils allowed medusahead to complete its life cycle.

Building on the work of Fosberg and Hironaka, I sampled the plant communities in the medusahead invasion area along the western edge of the Great Basin (Young and Evans 1970). Medusahead was found on the margins of many degraded meadows where moisture relationships probably favored it over cheatgrass. A much larger area of infestation was sagebrush/grass communities. The sagebrush communities consisted of mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana*) on soils with sandy loam to loam-textured surface horizons and often well-developed argillic horizons. A second series of sagebrush communities consisted of low sagebrush (*A. arbuscula*) growing on soils with clay-textured surface horizons. Harry Summerfield (retired soil scientist, Soil Conservation Service and Forest Service, USDA) suggests the low sagebrush soils share the same development as the big sagebrush soils, but the surface horizons have been removed by erosion (personal communication). On the Modoc Plateau of northeastern California these two series of plant communities divide the landscape about equally (Young et al. 1977). In the northern Great Basin low sagebrush constitutes only about 10% of the total sagebrush vegetation.

On the western edge of the Great Basin, medusahead, in nonmeadow situations, is largely restricted to low sagebrush potential plant communities. Would this restriction to clay soils change over time as appears to have happened in cismontane California? Remember the studies of Raymond Evans that showed competition in the cismontane portion of the California annual grasslands is initially for light, while in cheatgrass communities of the Intermountain area, competition is overwhelmingly for soil moisture (Evans et al. 1970, 1975).

Wildfires

Accumulations of litter, on areas where medusahead is established, will burn. McKell, Wilson, and Kay (1962) had initial results that seemed to indicate that burning was the answer to the control of medusahead. The idea was to burn stands while competing annual grasses were fully mature and medusahead seeds were still in the inflorescences. This study showed burned seeds would not germinate. However, the burned seeds were apparently incubated at 20 C, and unburned fresh seed would not have germinated at that temperature. We tried a series of burning experiments on the Pitt River Indian reservation and found burning favored medusahead (Young et al. 1972). We helped Forest Service range conservationists evaluate burning treatment on low sagebrush communities on the Silver Lake district of Fremont National Forest in Oregon; the off-season burns appeared to favor remnant perennial grasses over medusahead.

Low sagebrush communities, because of lack of herbaceous cover, are relatively resistant to the spread of wildfires. Big sagebrush communities, especially those with cheatgrass understories, are very subject to the spread of wildfires. Invasion of medusahead into low sagebrush communities introduces wildfires to these communities, perhaps for the first time since they were in pristine condition. Perennial grass, forb, and shrub cover are all negatively correlated with medusahead cover in the western Great Basin (Young and Evans 1970).

GRAZING PREFERENCE

It is obvious from the above discussion that preference by grazing animals plays an important part in the successional dynamics of medusahead communities. One of the few studies of medusahead palatability was conducted on the northern coast of California using sheep in small hurdle plots (Lusk et al. 1961). Under the confined conditions of the study, sheep utilized medusahead when it was green. When faced with no choice, they used some herbage after the medusahead matured. How much utilization of medusahead would occur in temperate desert situations is unknown.

Cheatgrass stands put a tremendous production of grass caryopses into a local ecosystem. Vertebrate granivores have adapted to this food source. Savage et al. (1969) showed in feeding trials that Chukar Partridges (*Alectoris graeca*) could not utilize the caryopses of medusahead as a food source. These birds are dependent on cheatgrass seeds in the fall and winter. We do not know what the influence of medusahead invasion would be on other granivores. Seeds of other recently introduced weeds in temperate desert communities, such as those of barbwire Russian thistle (*Salsola paulsenii*), are heavily preyed upon by granivores. If cheatgrass populations crash because of replacement by medusahead, what happens to cheatgrass seed predators?

A study conducted at Washington State University illustrates that granivore preference works both ways in plant succession. Bird populations prefer the seeds of native perennial grass species over those of cheatgrass and medusahead (Goebel and Berry 1976).

Utilization of medusahead by large herbivores of infested ranges results in increased incidence of injury from the seeds. Data on the level of injury are not available for domestic livestock and certainly not available for wildlife.

CONTROL OF MEDUSAHEAD

Kay developed highly technical and very successful control and revegetation techniques for the annual-dominated rangelands of cismontane California using the herbicide paraquat (1,1′-dimethyl-4,4′ bipyridinium ion) and specialized seeding equipment (Kay 1963, 1966, Kay and McKell 1963).

This technique was not successful in the Intermountain area because medusahead plants were not susceptible to paraquat in the temperate desert environment and the annual legumes that proved so adapted to cismontane California were not adapted to the sagebrush environment (Young et al. 1971b). Herbicidal fallow techniques using atrazine (6-chloro-N-ethyl-N′-[1-methylethyl]-1,3,5,-triazine-2,4-di amine) or dalapon (2,2-dichloropropanoic acid), and mechanical fallow techniques were developed for use in the Great Basin. Hilken and Miller (1980) provide a summary of herbicidal control measures applied experimentally for the control of medusahead. A large part of the area infested with medusahead in the western Great Basin was never adapted to these treatments because of surface rock cover that prohibited tillage or seed-drilling techniques. The current mass cancellation of federal registration for uses of herbicides on rangelands and the failure of federal land management agencies to adopt the use of herbicidal revegetation techniques have made the use of these techniques impossible. Landforms and soils of the sites where medusahead is spreading into temperate desert rangelands are critical factors in the ecological suppression of this species.

NATURE OF MEDUSAHEAD-INFESTED LANDSCAPES

The landscape of the western Great Basin where medusahead has invaded is composed of a series of fairly recent basalt flows that comprise the Modoc Plateau and the extreme southern extension of the Columbia River Basalts. Superimposed on the flows are clays from a Tertiary-age lake. This lake was much older than pluvial Lake Lahontan, which lapped at the lower margins of the flows. The old lake left thick beds of clay-textured sediments occasionally interbedded with diatomaceous earth. The clay minerals are predominantly double lattice forms that expand and contract with moisture content. This expansion and shrinkage has sorted basalt rock from the buried flows into giant polygons and pressure ridges until portions of the landscape resemble arctic ice packs that are black instead of white.

There are a host of topoedaphic situations within this wilderness that support specific assemblages of plants; however, the landscape is characterized by upland areas of residual soils with loam-textured surface soils that support big sagebrush and clay-textured surface soils that support low sagebrush. Vast, nearly level benches of lake sediments support swirling mosaics of basin big sagebrush (*Artemisia tridentata* ssp. *tridentata*) and a recently discovered type of sagebrush, a subspecies of low sagebrush known as Lahontan sagebrush. The basin big sagebrush occurs in depressions where erosional products accumulate on soils with clay-textured surface horizons, a very unusual occurrence for the Great Basin. The Lahontan sagebrush communities occur on the lake bed clay sediments that are veneered with thin layers of subaerially deposited, coarser-textured soil.

Wind erosion products accumulate under the shrub canopies and, coupled with organic matter from leaffall, build mounds under the shrubs while miniplayas develop in the interspaces. Eckert et al. (1989) have described and experimented with the seedbeds of these mound interspace situations, particularly the vesicular crust that forms in the interspaces and limits establishment of perennial grass seedlings.

The area of medusahead invasion in the western Great Basin is a microcosm where events in soil and plant ecology that influence millions of acres in the Intermountain area are brought, by fortuitous combinations of physical and biological parameters, into sharp focus. In the medusahead invasion area, lake-deposited red clay is in obvious discontinuity with the thin, gravish surface soil. In undisturbed profiles of this situation the influence of alleviation of subaerial deposited material is apparent on the structure of the clay subsoil, indicating the antiquity of this process (personal communication, Robert Blank, soil scientist, ARS, USDA).

Accumulations of medusahead litter change wildfire characteristics, and the shrub component of the plant community is eliminated. Continued grazing of medusahead-dominated grasslands is extremely deleterious on remnant perennial grasses because of differential grazing preference. In contrast to medusahead, cheatgrass is seasonally preferred forage species, and even the dry herbage of cheatgrass is utilized by livestock. This *dilutes* the effect of grazing as far as the native perennials are concerned. Lack of preference for medusahead *concentrates* the effects of herbivory. Subaerially deposited surface soil is extremely erodible once protection of the shrub canopy and its dependent microphytic crust is lost. Loss of the surface leads to exposure of the clay sediments that then function as Vertisols, shrinking, cracking, and swallowing the surface and reexpanding with moisture. Medusahead is one of the few plant species adapted to these Vertisols. Perhaps some of the soils of these landscapes were always Vertisols where, in wet years, annual sunflowers (*Helianthus annuus*) and turkey mullein (*Eremocarpus setigerus*) formed the only native vegetation. Perhaps excessive grazing converted some of these soils to Vertisols before medusahead arrived. The important point is that medusahead is actively attacking assemblages of native vegetation and changing the physical and biological potential of the sites.

MANAGEMENT OF MEDUSAHEAD INFESTATIONS

It is difficult to revegetate Vertisols in desert environments with both seedlings of woody and herbaceous species, native and exotic. Not only establishment but also subsequent growth are problems on these soils despite both tremendous cation exchange capacity and moisture-holding capacity. The tremendous matric potential of these fine clay soils is always surprising. Moisture is not available for normal plant growth when soils still stick to your boots.

NATURAL SUCCESSION

Dr. Min Hironaka suggests that over prolonged periods perennial seedlings might establish in medusahead-infested sites, especially the short-lived perennial grass squirreltail (Hironaka 1963). Dr. Hironaka and his students followed this aspect of medusahead succession in several studies. He demonstrated that squirreltail can establish in medusahead communities, but he found the perennial grass populations to be cyclic. When the squirreltail plants die, they are replaced by medusahead, not longer-lived perennial grasses (personal communication).

In the western Great Basin, Dr. Hironaka's work is borne out by gradual increases in squirreltail plant density as grazing management systems have been implemented. This has been especially noticeable during the past four years of extreme drought. Densities of one squirreltail plant per 10 square feet began to change the aspect of medusahead-dominated sites, but the fragile nature of this improvement is apparent when bioassay of seed banks shows 250–500 viable medusahead seeds per square foot (down from 1000 per square foot before the drought) and fails to detect any viable squirreltail seeds (unpublished research ARS, USDA, Reno, Nevada).

As you look at medusahead-infested areas on the Vertisols of the western Great Basin, you have a nagging thought that something is missing. The Lahontan and big sagebrush communities of the ancient lake sediments have as their most frequent perennial grass Sandberg bluegrass. This species is completely absent from the medusahead stands and is missing from the stands where squirreltail has begun to return. What factors of seedbed quality exclude the native invader Sandberg bluegrass and are the same factors related to the failure of higher-level perennial grasses to become established in squirreltail/medusahead communities?

The striking difference between native and medusahead communities, other than loss of shrub canopies, is loss of subcanopy mounds and microphytic crust that covers the mounds to extend down to mingle with vesicular crust in the interspaces. The thallophytic crust of mosses, lichens, and liverworts is obviously gone, and we can only speculate on the fate of the microscopic crust of algae, fungi, and bacteria. Prolonged medusahead dominance may decrease populations of mycorrhizae spores in the soil and thus influence growth of artificially established perennial seedlings (personal communication, Jim Trent, soil microbiologist, ARS, USDA, Reno, Nevada).

Specific plant pathogens, developed and marketed by biotechnological companies, may have a role in range weed control. Perhaps a *Fusarium* species exists that would be highly specific for medusahead (personal communication, Joe Antognini, National Program scientist, Weed Science, ARS, USDA).

Taxonomists and geneticists who have worked with medusahead have commented on how variable individual collections may be. Common garden studies have shown this to be true for collections from the American West (McKell, Robinson, and Major 1962, Young et al. 1971b). We found, in common garden studies, a collection from northern California that matured 4 weeks earlier than the average for other collections or on or before the maturity for cheatgrass. As medusahead evolves, we have yet to see the limits of its potential on the western range. The recent discovery of medusahead in Utah illustrates that portions of the eastern Great Basin have the potential to be invaded by this weed (Horton 1991).

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ROOST SITES USED BY SANDHILL CRANE STAGING ALONG THE PLATTE RIVER, NEBRASKA

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Abstract.—We assessed the influence of water depth, extent of unobstructed view, and human disturbance features on use of roost sites by Sandhill Cranes along the Platte River, Nebraska, during spring migratory stopover. Aerial photos taken near dawn were used to determine areas of flock use and habitat availability in four sample reaches, and measurements were made on the ground at flock roost areas. In general, depths of 1–13 cm were used by sandhill cranes in greater proportion than those available. Exposed sandbars and depths >20 cm were avoided, while depths of 14–19 cm were used in proportion to their availability. Sites 11–50 m from the nearest visual obstruction were used significantly greater than their availability, while sites 0–4 and >50 m from visual obstructions were avoided. Sandhill Cranes avoided sites near paved roads, gravel roads, single dwellings, and bridges when selecting roost sites; however, they did not appear to be disturbed by private roads, groups of residential buildings, gravel pits, railroads, or electrical transmission lines.

Key words: Sandhill Crane, Grus canadensis, *river roosts, habitat selection, water depth, disturbance, sandbars, Platte River.*

The impact of water resource development on the Platte River is well described (Kroonemeyer 1978, Williams 1978, Eschner et al. 1981, Kircher and Karlinger 1981, U.S. Fish and Wildlife Service 1981, Krapu 1987, Sidle et al. 1989). The major impact has come from irrigation projects along the North Platte River (Krapu et al. 1982), which remove approximately 70% of the annual flow of the Platte River before reaching south central Nebraska (Kroonemeyer 1978). Concomitant with channel shrinkage, woody vegetation has encroached on thousands of hectares of former channel area, contributing to further changes in channel features and altering habitat for numerous species of migratory birds in the Big Bend Reach of the Platte River in Nebraska (U.S. Fish and Wildlife Service 1981). The Big Bend Reach of the Platte River in Nebraska is an area of importance to numerous species of migratory birds of the Central Flyway (U.S. Fish and Wildlife Service 1981).

This area is an important stopover area for most of the midcontinent population of Sandhill Cranes (*Grus canadensis*) (400,000–600,000 birds), which roost in the river and feed in nearby corn fields (Krapu et al. 1981, Krapu 1987). The endangered Whooping Crane (*G. americana*) also uses the area during migration, and the threatened Bald Eagle (*Haliaeetus leucocephalus*) is a common winter resident (U.S. Fish and Wildlife Service 1981). The area is also important habitat for the endangered interior population of Least Tern (*Sterna antillarum*) and the threatened Piping Plover (*Charadrius melodus*), both of which nest along the Platte River (U.S. Fish and Wildlife Service 1981, Sidle et al. 1989).

Considerable attention has been given to the impact of changing channel conditions on the midcontinent population of Sandhill Cranes (*Grus canadensis*) that congregate along the river from early March to mid-April during their annual spring migration (Lewis 1977, Krapu 1978, U.S. Fish and Wildlife Service 1981). During this time approximately 400,000 Sandhill Cranes use this area while enroute to their breeding grounds in Canada, Alaska, and eastern Siberia (U.S. Fish and Wildlife Service 1981).

In Nebraska various facets of Sandhill Crane roosting habitat requirements have been studied (Frith 1974, Lewis 1974, U.S. Fish and Wildlife Service 1981, Krapu et al. 1982, 1984). However, these studies have not considered the influence of habitat availability in relation to habitat use. The purpose of this study was to

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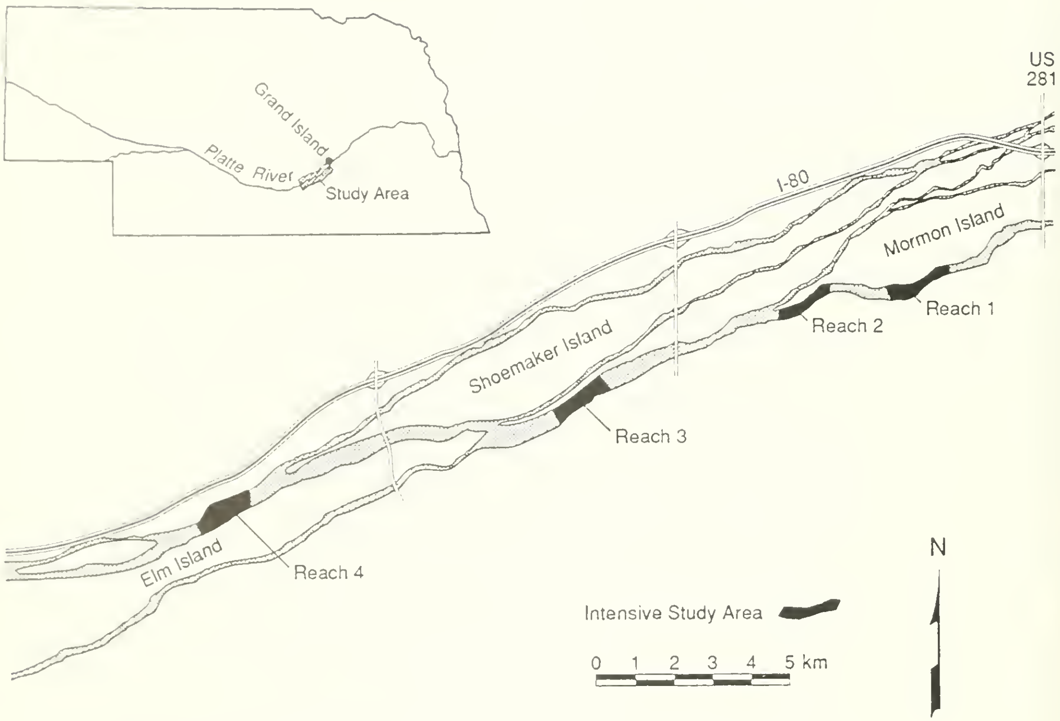

Fig. 1. Study sites in the Platte River, Nebraska.

determine the influence of habitat availability, as well as habitat use, on the selection of roost sites by Sandhill Cranes.

This study was designed to assess the influence of three types of habitat features on roost sites used by Sandhill Cranes: (1) water depth, (2) magnitude of unobstructed view, and (3) disturbance features.

STUDY AREA

The study area is located in south central Nebraska in Hall and Buffalo counties in the eastern half of the Big Bend Reach of the Platte River. It encompasses a 36-km stretch of the Platte River beginning 4 km west of Shelton to Grand Island (Fig. 1). All field measurements were in four 1.6-km reaches along the main channel of the Platte River.

Spring precipitation in Nebraska contributes to the Platte River Basin flow but most of the flow is derived from spring runoff that originates as snowmelt in the Rocky Mountains (Eschner et al. 1981). Spring runoff flows into both the North and South Platte rivers, which flow northeast and southeast respectively, across the Great Plains to their confluence near North Platte, Nebraska.

The study area is characterized by numerous braided channels interspersed with unvegetated sandbars that frequently shift. Most of the land within and adjacent to the study area is in private ownership. Land use in the area is predominantly agriculture and includes approximately 60% cropland (mostly corn), 5% tame pasture, 20% native grassland, and 15% riparian woodland (Reinecke and Krapu 1979).

The riparian woodland comprises eastern cottonwood (*Populus deltoides*) forests with dominant understory species of red cedar (*Juniperus virginiana*) and rough-leaf dogwood (*Cornus drummondii*). On low islands and vegetated sandbars, peach-leaf willow (*Salix amygdaloides*), coyote willow (*S. exigua*), and indigo bush (*Amorpha fruticosa*) are the dominant species (U.S. Fish and Wildlife Service 1981, Currier 1982).

METHODS

Aerial photography was used to determine flock locations and delineate flock boundaries of roosting Sandhill Cranes along a 36-km stretch of the Platte River. Photography was restricted to mornings with less than 10% cloud cover and ceilings above 975 m. Flights were begun 30 minutes before sunrise because of the need to photograph Sandhill Cranes before they leave the roost in early morning. Light was adequate to permit photography 10–15 minutes before sunrise.

A Hasselblad 500 EL, 70-mm camera was used to photograph the study area. The camera was mounted in a standard camera hatch in a Cessna 172 fixed-wing aircraft and was equipped with an 80-mm focal length Zeiss lens. Exposures were made at 1/60 and 1/125 second at f2.8 using Kodak Tri-X 640 AFS Aerographic film. The camera was equipped with a 70 exposure back loaded with 5.5 m of film allowing 80 exposures.

The aircraft was flown at approximately 140 km/hr at an initial altitude of 790 m above ground level for the first two flights. During the last two flights the altitude was increased to 910 m above ground level. These altitudes provided a 0.48-km^2 and 0.64-km^2 coverage on each frame, respectively. Frame rate was controlled by an intervalometer, calibrated for 30% overlap, to provide continuous photographic coverage of the study area.

Shortly after each flight the film was custom processed by hand agitation in a single solution tank, varying time and developer temperature to obtain optimum development. Approximately 150 frames were exposed from each flight. Frames were examined under 8X magnification to identify crane flocks and were enlarged to 41 × 51 cm (16 × 20 in) and printed on Kodak Poly contract RC paper. Processed photographs were stored for later analysis of visual obstructions and disturbance features.

Each of the four 1.6-km reaches was marked on both sides of the river bank with 16, 1-m^2 markers made of white cloth. The markers, placed 100 m apart at the edge of the river bank, were positioned in such a way that markers on the opposite sides of the channel were parallel to the channel. The markers enabled accurate scale measurements to be taken from photos and provided position reference for transects across the channel when sampling water depths. Aerial photographs covering each reach were used to determine the position of transects through flocks. Transects were positioned so that each flock studied on a photo was divided into general areas of equal size with two to five transects depending upon flock size. A flock was defined as a continuous distribution of birds or an aggregation of birds spatially independent of other birds separated by a distance >20 m. Flocks usually occurred in configurations that appeared distinct from other flocks in the vicinity.

After transects were located on photographs, they were measured and laid out on the ground in relation to marker locations using vinyl flagging placed on each side of the channel. Water depths were measured to the nearest 3 cm at 3-m intervals and plotted on acetate overlaid on aerial photographs with delineated flock boundaries. Width and depth data were combined to give mean estimates for each of the four reaches.

Each 1.6-km reach was sampled as soon as possible after each flight, always within three days. Staff gauges were placed in each area to measure any changes in water level between the time each reach was photographed and the time it was sampled. Detectable changes in water level were recorded and used to correct depth distributions.

Discharge was measured on each flight day in close proximity to the study areas following the technique of Buchanan and Somers (1969).

Contact prints were made from each roll of film. Individual frames were cut out and glued onto posterboard to form a mosaic, providing a continuous coverage of the river channel. Scale was determined by comparing bridge segments and transect locations on the contact prints with measurements of these locations made on the ground. Scale estimates were made along 2- to 3-km segments of river. Photograph scales ranged from 1:8,681 to 1:10,334 for the first two flights, and 1:10,595 to 1:11,857 for the last two flights.

A binocular zoom microscope (1–4X) was used to identify flocks and delineate flock boundaries on the contact prints covered with acetate. Flocks were delineated and subsequently numbered on the acetate overlays on contact photos. The distance from the edge of each flock to the nearest visual obstruction was measured to the nearest 0.5 mm on the photos (ground distance = 4–6 m) using a drafting caliper. Visual obstructions included vegetation, a river bank, or any other "visually solid" object >1 m in height.

Random points were plotted on contact photos to estimate the features of available habitat. Random points were determined by a series of random numbers identifying point coordinates on gridded overlay covering contact prints. Points outside the river channel were discarded. Only random points located in water were used because points on sandbars, islands, or the river bank were not considered potentially usable roosting habitat. A total of 339 random points within the river channel were identified on the contact prints. Grid squares were 1.25 mm^2 to ensure a representative sample of locations on the river. As with flock locations, the distance from each random point to the nearest visual obstruction was measured on the photos to the nearest 0.5 mm using a drafting caliper.

For analysis of human disturbance features, flock locations and random points along the entire 36-km study area were transferred from 70 mm contact prints to acetate overlays of color infrared aerial photographs (scale 1:25,595) using a zoom transfer scope. The photographs taken in April 1989 were obtained from the Bureau of Reclamation in Grand Island, Nebraska. Distances were measured from the edge of each flock and individual random points selected by placing a card over the photograph to the nearest human disturbance features. These features included paved roads, gravel roads, private roads, urban dwellings, single dwellings, railroads, commercial development, highways, and bridges. Distances were measured to the nearest 0.5 mm on photos (ground distance = 13 m) with a drafting caliper.

Data Analysis

Frequency histograms were plotted for measured distances from the edge of a flock and for random distances to the nearest visual obstruction and disturbance features. Frequency distributions were plotted for available and used selected water depths. Frequency distributions of available and used selected water depths for each 1.6-km reach were determined by combining flock data for each reach for a given flight. Available depths were defined as all depth measurements taken along a transect, and used depths were those depths where birds were present along a transect. Habitat selection was computed by dividing the proportion of habitat used within a depth interval by the proportion of depths available in that same interval (Bovee 1986). Depths used less than their availability were defined as being avoided while those used more than their availability were defined as being selected. Habitat availability, use, and selection were summarized within reaches, across flight dates, and from data pooled across reaches and flight dates. Data were pooled to generalize the selection of depths over the course of the sampling period.

The chi-square of homogeneity (Marcum and Loftsgaarden 1980) was used to test whether differences existed between the distribution of random points and those locations used by Sandhill Cranes relative to visual obstructions and disturbance features. It was also used to determine if there were differences between the proportion of used and available water depths among and within reaches. Confidence intervals were calculated using the Bonferroni *Z*-statistic to test which intervals within the distributions were used more or less than expected (Byers et al. 1984). Differences between selection functions were tested with a *Z*-test. Analysis of variance (ANOVA) was used to determine if visual obstructions had an effect on the disturbance potential created by various types of disturbance features. Significance for all statistical inferences was $P \leq .05$.

RESULTS

A total of four sampling flights were made: one each on 21 and 31 March and 4 and 10 April 1989. A total of 285 flocks were identified during the four flights. Following the flights, 20 flock sites were selected and sampled and a total of 5109 depth measurements were recorded in the field.

SAMPLING AREAS.—Reaches I and II were the narrowest, with mean channel widths of 254 m (range = 225–319 m) and 249 m (range = 241–263 m), respectively, while reaches III and IV, located upstream, were wider. Reach III had a mean channel width of 413 m (range = 387–440 m), while reach IV had a mean channel width of 357 m (range = 296–445 m).

Reaches I and II had similar discharge (17 m^3/s), while reaches III and IV had greater values (27 and 44 m^3/s) on 21 March (Table 1). Discharge in reach III was typically twice as high as reaches I and II. Reach IV had the highest discharge of the four reaches, often three times greater than in reaches I and II (Table 1). Reaches I, II, and III were located in a braided portion of the surface along the south channel and contained only partial river flow.

TABLE 1. Discharge in cubic meters per second (m^3) for sample reaches on different flight dates along the Platte River, Nebraska, during spring 1989.

Flight date	Reach I	Reach II	Reach III	Reach IV
21 March[a]	17.4	17.4	27.5	44.6
31 March	11.1	—	18.6	32.1
4 April	10.6	10.6	—	28.8
10 April	7.9	7.9	13.7	21.7

[a] Discharges for all reaches on 21 March were measured on 24 March. Thus, a three-day lag period existed between the time each reach was flown and the time each reach was measured for discharge.

Reach IV was located along the main channel and contained total river flow.

HABITAT AVAILABILITY.—The distribution of available water depths differed among reaches. On 21 March 1989, 82% of the available habitat in reaches I and II consisted of depths 0–25 cm. In contrast, 53% and 66% of the available habitat in reaches III and IV, respectively, consisted of depths 0–25 cm.

An increased frequency of shallow depths (0–19 cm) and a decreased frequency of deeper depths (>20 cm) occurred over the study period. This division is made because cranes seldom used depths greater than 20 cm. The increase in exposed sandbars (depth = 0 cm) was most pronounced in reaches I and II, which showed increases of 13% and 11%, respectively. Reaches II and III showed increases of 12% and 19%, respectively, in available depths of 1–4 cm between the first and last flight. Reaches III and IV showed decreases of 10% and 7%, respectively, in depths >38 cm for the same period. During the study period a progressive decrease in discharge occurred (Table 1), causing more shallow areas (0–19 cm).

HABITAT USE.—Frequency distributions of roosting habitat use by cranes indicated the highest proportions of used water depths were from the 1–4 and 5–7 cm increments. This range of water depth accounted for 65% of the measured depths. There was no discernible variation in the frequency of water depths used among the four reaches.

There was a small, but significant, difference in the distribution of depths used between the beginning and end of the study period ($P < .05$). Depths of 0 cm showed a significant decrease in use, while depths 20–22 cm showed a significant increase in use ($P < .05$). The data showed a significant difference between the distribution of used and available water depths for all four sampling periods ($P < .001$). Sandhill Cranes used progressively deeper water depths as the study season progressed. Depths >20 cm were used significantly less than expected during the first flight; but, by the last survey, only depths >29 cm were used less than expected ($P < .05$). Depths of 0 cm were generally avoided by Sandhill Cranes during the last two surveys and were used less than would be expected by chance ($P < .05$).

Habitat selection was assessed using both habitat use and availability data for specific water depths. The most frequently occurring depth intervals for which selection occurred were 5–7 cm, followed by 1–4, 8–10, 11–13, and 14–16 cm in decreasing order of preference.

VISUAL OBSTRUCTIONS.—There was a significant difference between the distribution of flock locations and random points relative to the distance from the nearest visual obstruction ($P < .001$). Proportional use of sites 0–50 m from the nearest visual obstruction was significantly greater than availability ($P < .05$), while sites >50 m from a visual obstruction were avoided ($P < .05$).

The 0–25 m interval was divided into six increments: 0, 1–4, 5–10, 11–15, 16–20, and 21–25 m. There was a significant difference between the distribution of flocks and random point distances ($P < .001$). Sites as close as 5–10 m from the nearest visual obstruction were used by Sandhill Cranes. Only sites 0–4 m from a visual obstruction were avoided ($P < .05$), while sites 11–25 m from a visual obstruction were used more than expected ($P < .05$).

Visual obstructions were divided into three categories: (1) unvegetated bank, (2) vegetated bank, and (3) vegetated island. There were no significant differences in the distribution of distances between an unvegetated and vegetated bank, but there were significant differences for the distribution of distances between vegetated banks and vegetated islands and between unvegetated banks and vegetated islands ($P < .005$). Sandhill Cranes roosted a mean distance of 45 m from unvegetated banks, 50 m from vegetated banks, and 27 m from vegetated islands.

CHANNEL WIDTH.—There was a relationship between the minimum unobstructed channel width and distance to the nearest visual obstruction. The distance to the nearest visual obstructions was a function of less than one–half the minimum unobstructed channel width.

There was a significant difference between the distribution of flock locations and random points relative to minimum unobstructed channel width ($P < .005$). Sandhill Cranes used channels 100–200 m wide in greater proportion than those generally available. Channels narrower than 100 m were avoided, while those >200 m wide were used in proportion to their availability. The mean minimum unobstructed channel width used by roosting flocks was 196 m (range = 34–445 m). Nearly 100% of the flocks were in channels with a minimum unobstructed channel width of >50 m, and over 97% and 80% of the flocks were in channels with a minimum unobstructed width of >100 and >150 m, respectively. The mean relative flock size (surface area) was 3883 m^2 (range = 19–55,354 m^2). There was no relationship between flock size and minimum unobstructed channel width. Both large and small flocks were located in wide, as well as narrow, channels.

Human Disturbance Features

PAVED ROADS.—Sandhill Crane flocks were not distributed randomly with respect to distance from paved roads ($P < .001$). Sandhill Cranes showed avoidance of sites closer than 500 m from the nearest paved road ($P < .05$), but used sites as close as 301–400 m. Sites located 701–900 m from the nearest paved road were used more than expected ($P < .05$). Sandhill Cranes roosted a mean distance of 1260 m from the nearest paved road when a visual obstruction was present, but a mean distance of 1575 m from the nearest paved road in the absence of visual obstructions.

GRAVEL ROADS.—There was a significant difference between the distribution of used sites and random locations relative to distance from gravel roads ($P < .01$). Sandhill Cranes showed avoidance of sites that were closer than 400 m from the nearest gravel road ($P < .05$), but flocks were located as close as 301–400 m. Sites that were 601–800 m from the nearest gravel road were used more than expected ($P < .05$). The presence of visual obstruction between a roosting flock and the nearest gravel road did not appear to reduce the disturbance potential created by gravel roads.

SINGLE DWELLINGS.—There was a significant difference between the distribution of used and random locations relative to the distance to the nearest single dwelling ($P < .01$). In general, Sandhill Cranes showed an avoidance for sites closer than 400 m from a single dwelling ($P < .05$). Sites 501–600 m from the nearest single dwelling were used more than expected ($P < .05$). The presence of a visual obstruction between a flock and the nearest single dwelling did not affect the disturbance potential created by single dwellings.

BRIDGES.—Sandhill Crane flocks were not distributed randomly with respect to distance from bridges ($P < .001$). They showed avoidance of sites closer than 400 m from the nearest bridge ($P < .05$). Similarly, they used sites >400 m from the nearest bridge.

OTHER DISTURBANCES.—No significant differences were found between urban dwellings, gravel pits, commercial development, transmission lines, and the distribution of Sandhill Crane flocks.

DISCUSSION

DEPTH DISTRIBUTION.—This study indicated that Sandhill Cranes prefer water depths of 1–13 cm for roosting but roost in greater depths. Lataka and Yahnke (1986) developed a predictive model for Sandhill Crane roosting habitat and stated that the majority roosted in water depths between 0 and 12 cm, which is presumably the optimal depth for roosting. Similarly, Frith (1986) suggested a water depth of 2–15 cm as optimum for roosting sites. Currier (1982) reported a slightly deeper range of depths from 10–15 cm as optimum for roosting. Lewis (1974) suggested that roost sites be characterized by depths 10–20 cm, and Folk (1989) reported an even greater range of depths used for roosting: 0.1–21.0 cm for Sandhill Cranes along the North Platte River in Nebraska.

Despite a change in the availability of water depths with over a 50% reduction in discharge over the period of study (Table 1), only slight differences were detected in the overall use of specific water depths. The fact that habitat use remained the same despite a change in habitat selection suggests that selection indices more strongly refelect changes in habitat availability than habitat preference. If habitat selection had reflected habitat preference, then habitat selection indices would have been more similar between the beginning and end of the study period.

VISUAL OBSTRUCTIONS.—This study indicated that Sandhill Cranes will not roost closer than 5 m from a visual obstruction and that distances from 11 to 25 m are the most frequently used. Latka and Yahnke (1986) reported that Sandhill Cranes did not roost <15 m from the bank. Folk (1989) suggested that Sandhill Cranes preferred to roost >25 m from a visual obstruction, but he observed roosting as close as 4 m from a visual obstruction. Our results indicate that various forms of visual obstructions have different impacts on roost site selection. Overall, vegetated islands have little influence on the selection of roost sites, whereas vegetated banks have greater influence.

It is generally believed that Sandhill Cranes maintain an optimum distance from a visual obstruction to increase their security from terrestrial predators, primarily candids. This is evidenced by the fact that the majority of flocks are located in closer proximity to vegetated islands than to unvegetated or vegetated banks.

Channel morphology may also be a factor influencing the distribution of roosting areas relative to banks or islands. This assertion is supported by observations from depth measurements which suggest that water depths and velocities near banks are deeper and faster than depths near islands due to bank undercutting. Thus, sites near islands may contain a greater proportion of suitable roosting depths than sites adjacent to banks.

CHANNEL WIDTH.—Sandhill Cranes selectively used channels 100–200 m wide, while channels narrower than 100 m were avoided. Nearly 100% of the roosting Sandhill Crane flocks were located in channels with an unobstructed channel width >50 m, and over 80% were located in channels >150 m wide. Wide channels potentially provide more space for roosting Sandhill Cranes, more security from predators, and more available water depths to choose from. However, since channel width was evaluated independently of channel depth, it is possible that use of narrow channels (<100 m wide) is limited not so much by a requirement for wider channels, but by deeper water that flows through these channels (Latka and Yahnke 1986).

Our findings corroborate the results of Krapu et al. (1984), who reported that over 99% of all roosting Sandhill Cranes were in unobstructed channels over 50 m wide and almost 70% were in channels >150 m wide. In contrast, data from nighttime aerial thermography by Pucherelli (1988) suggested that almost half of all roosts were in channels <150 m wide and that the greatest proportion of roosts were in channels 51–150 m wide.

Folk and Tacha (1990) studied roosting along the North Platte River in Nebraska and reported a channel width criterion that was different from this study They reported that 82% of the roosts were in channels >48 m wide and 18% were in channels from 16–47 m wide.

HUMAN DISTURBANCE.—Our study demonstrated that human disturbance features influence selection of roost sites by Sandhill Cranes. In general, the greatest disturbance potentials were attributed to roads (paved and gravel), bridges, and single dwellings where irregular but considerable human activity might occur. Gravel pits, private roads, railroads, and power lines had infrequent disturbances and did not seem to affect roost site selection. In all likelihood some form of acclimation occurs between the constant disturbance on commercial and urban development.

There is little literature that objectively describes the zones of influence exerted by various human disturbance features on the selection of roost sites by Sandhill Cranes along the Platte River. Folk (1989) suggested that riparian forest along the river provides a visual barrier against most types of potential disturbances and that Sandhill Cranes roost in sections of the river as close as 80 m from a bridge. In contrast, our study indicates that Sandhill Cranes roost in sections of the river that are >400 m from the nearest bridge. We feel that our results provide an objective description of potential zones of influence exerted by various disturbance features and the effect these features have on roost site selection by Sandhill Cranes along the Platte River.

In summary, our study shows the importance of sandbars with water less than 20 cm in depth surrounded by deeper water. These sandbars must be at least 5 m from some form of visual obstruction such as dense vegetation. This apparently allows the Sandhill Cranes to see approaching predators. As a result, Sandhill Cranes normally roost in channels 100–200 m wide. These sites are generally away from human disturbances such as roads, bridges, and private dwellings. Sandhill Cranes could tolerate irregular disturbances such as private roads and railroads.

The fact that 80% of the midcontinent population of Sandhill Cranes uses this area for staging in the spring indicates its importance. It is during this period that the birds apparently build up energy reserves allowing them to continue their northward migration. If the area were to become unfit for Sandhill Cranes, the population would likely suffer decline.

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POST-PLEISTOCENE DISPERSAL IN THE MEXICAN VOLE (*MICROTUS MEXICANUS*): AN EXAMPLE OF AN APPARENT TREND IN THE DISTRIBUTION OF SOUTHWESTERN MAMMALS

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ABSTRACT.—The present distribution of the Mexican vole (*Microtus mexicanus*) is not entirely the product of post-Pleistocene forest fragmentation and extinction; recent dispersal also is indicated. Literature records further suggest that this phenomenon may reflect a general pattern of northward range expansion in many southwestern mammal species.

Key words: Microtus, *vole, dispersal, biogeography, vicariance, Pleistocene.*

Traditional biogeographic theory attributes the modern distribution of small, nonflying montane mammals in the Southwest to post-Pleistocene climatic change (Brown 1971, 1978, Patterson 1984, Patterson and Atmar 1986). Restriction of woodland and forest habitat to higher elevations is assumed to have stranded such species on isolated patches of montane habitat. Although it is recognized that local extinction has caused further range reductions, post-Pleistocene range expansion generally has been discounted (Brown 1971, 1978). This relict model satisfactorily explains the distribution of many Great Basin species, but evidence from elsewhere in the Southwest strongly supports recent dispersal (Davis and Dunford 1987, Davis and Ward 1988, Davis et al. 1988, Davis and Bissell 1989, Davis and Brown 1989, Lomolino et al. 1989).

In this paper we will review evidence indicating that many southwestern mammals—including the Mexican vole and other montane mammals, as well as nonmontane species—have shown a striking northward range shift during the past several decades. For some species this pattern appears to reflect milder winters or human influences; for others the trend is harder to explain. If verified, however, this trend presupposes (among other things) a greater dispersal capability than is typically attributed to small mammals.

DISPERSAL: A BRIEF REVIEW

Post-Pleistocene dispersal has been verified primarily in (1) conspicuous, diurnal mammals such as sciurids and (2) mammals colonizing regions that were previously well sampled by collectors. For species and groups that do not fall into either category, the biogeographer is left to interpret broader distribution patterns and/or small bits of indirect evidence.

As an example of the first situation, Davis and Brown (1989) and Davis and Bissell (1989) showed that recent dispersal has significantly altered the distribution of Abert's squirrel (*Sciurus aberti*). Another example involves the dusky chipmunk (*Tamias obscurus*), which was absent from Thomas Mountain in southern California at least between 1974 and 1976 (Callahan 1977). By 1979 the species had recolonized this peak, which is isolated from the San Jacinto range by a 10-mile stretch of semiarid grassland/sagebrush habitat (Callahan, in preparation). The second scenario is illustrated by Davis and Dunford (1987) and Davis and Ward (1988), who found evidence of recent montane colonization by *Sigmodon ochrognathus* in a well-studied area of southeast Arizona.

Since many small mammals are not readily trapped and many localities have not been sampled extensively, it is easy for critics to "shoot down" new distribution records on the grounds of inadequate prior sampling. In such cases it is

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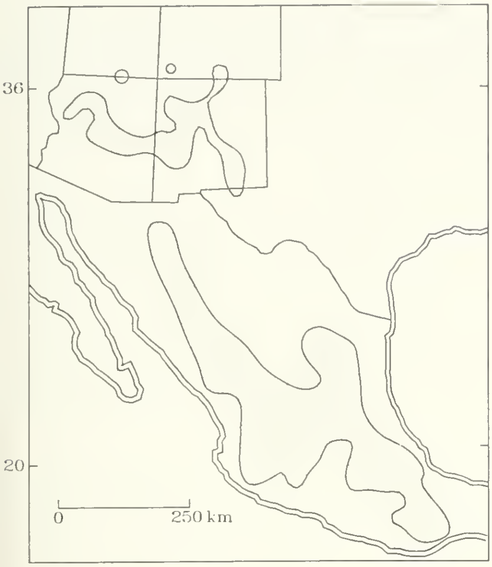

Fig. 1. Distribution of *Microtus mexicanus*. At this scale, only the two most isolated populations in the United States are distinguished (modified from Findley et al. 1975, Hall 1981, Finley et al. 1986, Hoffmeister 1986).

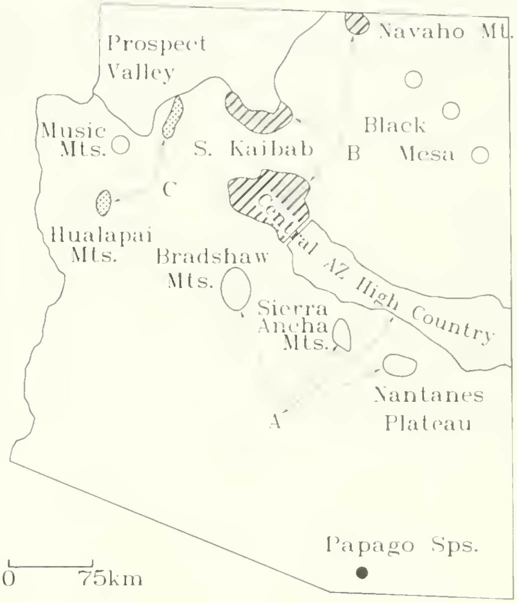

Fig. 2. Details of the distribution of *Microtus mexicanus* in Arizona showing isolated populations and three subspecies A, B, and C (modified from Hoffmeister 1986). Open circles indicate records added by Spicer et al. (1985) and Spicer (1987); subspecific relationships of these populations are unknown. Papago Springs is a late Pleistocene fossil site which includes a tentative record for this species (Harris 1985).

necessary to look at broader distribution patterns and draw some reasonable inferences. Davis et al. (1988) analyzed southwestern montane mammal distributions and found that distance from the source was a significant predictor of species richness—a relationship suggesting dispersal. Lomolino et al. (1989), in a study encompassing much of the Southwest, confirmed the relationship between species richness and isolation, and proposed recent dispersal by several montane species including *Microtus mexicanus*.

MEXICAN VOLE DISTRIBUTION

The range of the Mexican vole (Fig. 1) presently extends from Mexico into Arizona, New Mexico, southern Colorado, and Utah (Durrant 1952, Armstrong 1972, Findley et al. 1975, Hall 1981, Hoffmeister 1986). The species typically nhabits meadows in ponderosa pine and mixed conifer forests, but can occupy pinyon-juniper woodland if suitable understory is present Harris 1985, Hoffmeister 1986). In Arizona it occurs less often in interior chaparral and Great Basin desertscrub (Hoffmeister 1986).

The late Pleistocene distribution of this species probably was continuous from the Mexican lateau to the southwest U.S. (Findley and Jones 1962). Harris (1985) questions a fossil record from southeast Arizona that would confirm this past distribution, but the present disjunct range of the species (Fig. 1) implies its former presence in southeast Arizona regardless of the fossil record. Post-Pleistocene climatic changes fragmented this distribution, and local extinctions in southeast Arizona apparently separated the Mexican and northern populations. This scenario is consistent with the historical legacy hypothesis, but there is also evidence that the pattern has been modified by recent dispersal as discussed below.

EVIDENCE FROM ARIZONA.—The Mexican vole now occurs in the continuous forests of central Arizona and on isolated mountains to the south, southwest, and north (Figs. 1, 2). Four populations occur on mountains connected to the central high country by pinyon-juniper woodland and interior chaparral (Brown and Lowe 1983), through which the species could disperse: the Nantanes Plateau, the Sierra Ancha, the Bradshaw Mountains, and the South Kaibab (Fig. 2). Three other populations occur at sites that are isolated by grasslands but

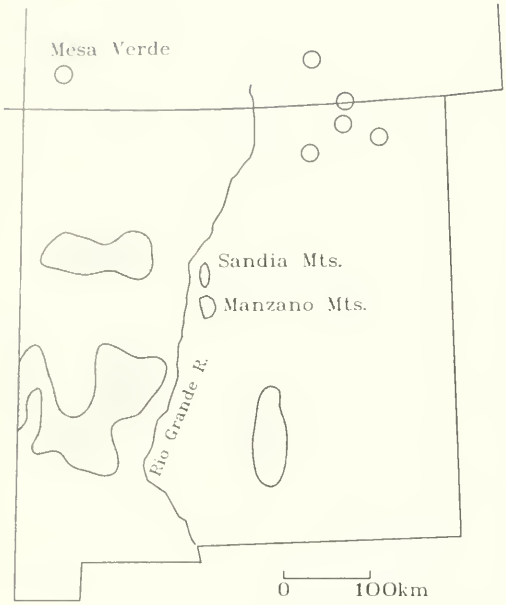

Fig. 3. Details of the distribution of *Microtus mexicanus* in New Mexico and southern Colorado showing some isolated populations (modified from Findley et al. 1975; some data from Hall 1981). Open circles indicate records listed by Finley et al. (1986).

interconnected by pinyon-juniper woodland and interior chaparral: Prospect Valley, the Music Mountains, and the Hualapai Mountains (Fig. 2).

Since the Hualapai Mountains and Prospect Valley still contain small patches of forest, the vole populations at these sites might be Pleistocene relicts in forest refugia. But the population in the Music Mountains, a site midway between the other two, consists of only pinyon-juniper woodland (Spicer et al. 1985). This habitat interconnects all three localities and is more likely to serve as a dispersal corridor than as a post-Pleistocene refugium. The species was recorded in the Hualapai Mountains in 1923 and in Prospect Valley in 1913, but it was not found in the Music Mountains until 1981 (Spicer et al. 1985).

When the rate of dispersal exceeds that of extinction, a species should be present on those montane islands closest to the source, assuming the species can cross the intervening habitat (MacArthur and Wilson 1967). The distribution of the Mexican vole in the Southwest generally fits this model (Fig. 2, Lomolino et al. 1989). In Arizona five pairs of closely related isolate populations occur in geographic proximity (Hoffmeister 1986). Recent dispersal is not the only possible explanation for this pattern, but it is the most parsimonious one; ancient relicts in dissimilar habitats would be expected to show more evidence of divergence after several thousand years.

There is evidence of a recent range expansion in northeast Arizona. The Mexican vole was first recorded in the Navajo Mountains in southern Utah and northern Arizona in 1933 (Benson 1935). Although this locality seems isolated, since 1986 the species has turned up at several other sites on Black Mesa in northeast Arizona (Spicer 1987). These sites fall on a line southeast from Navajo Mountain to the southwest foothills of the Chuska Mountains.

At Black Mesa (Fig. 2) the habitat is pinyon-juniper, with ponderosa pines and a few Douglas-firs on north-facing slopes, draws, and other protected areas (Spicer 1987). Again, this is relatively poor habitat for this species, and it seems unlikely that the population could have survived in isolation for several thousand years. Between these sites and Navajo Mountain is mostly pinyon-juniper, with narrow strips of northern grassland and Great Basin desertscrub (Brown and Lowe 1983). The Mexican vole occupies these habitats elsewhere and presumably can disperse through them. This scenario implies that the Chuska Mountains, now unoccupied by the species (Hoffmeister 1986), will eventually be colonized (or recolonized) from the northwest.

EVIDENCE FROM NEW MEXICO AND COLORADO.—Findley et al. (1975) suggested that the range of *Microtus mexicanus* in New Mexico could have expanded as a result of recent dispersal. In the Sandia Mountains, trapping from 1950 to 1970 revealed only *M. longicaudus*. Mexican voles were first taken there in 1970 and soon became the dominant species. While the species could have been overlooked earlier, dispersal from the Manzano Mountains (Fig. 3) is an equally likely scenario. Until 1975 these were the northernmost records east of the Rio Grande River in New Mexico. The Mexican vole has since been recorded from five sites in extreme northeast New Mexico (Dalquest 1975, Finley et al. 1986).

In Colorado the first specimens were taken in 1956 at Mesa Verde (Rodeck and Anderson 1956). Later the species was found at seven more Colorado sites (Fig. 3; Mellott and Choate 1984, Finley et al. 1986). A trapping study in

Table 1. Southern mammal species for which there is evidence of a recent northward range expansion. Unless indicated otherwise, evidence is based on directionality and chronology of records: **1**, Arizona distribution in Cockrum (1960) vs. Hoffmeister (1986); **2**, distribution in Hall and Kelson (1959) vs. Hall (1981); **3**, Texas distribution in Taylor and Davis (1947), Davis (1960), and Davis (1974). Nomenclature follows Jones et al. (1986).

Species	Region and direction of expansion	Evidence and References
Didelphis virginiana	N through E U.S.; N into S Arizona from N Mexico	Udvardy (1969), McManus (1974); Y. Petryszyn (personal communication)
Mormoops megalophylla	N in Texas	**3**; Taylor and Davis (1947); Davis (1960); Davis (1974); Mollhagen (1973)
Choeronycteris mexicana	Now a winter resident in S Arizona	R. Sidner (personal communication), probably due to hummingbird feeders
Leptonycteris sanborni	Now a winter resident in S Arizona	R. Sidner (personal communication), probably due to hummingbird feeders
Lasiurus ega	N in Texas	Spencer et al. (1988)
Idionycteris phyllotis	N in SW U.S. to Utah	First U.S. record was in 1955 in SE Arizona (Cockrum 1956); **2**
Tadarida femorosacca	N in Arizona	**1** and **2**
Tadarida macrotis	N in Arizona; also Texas?	**1**; Mollhagen (1973)
Dasypus novemcinctus	N from S Texas into Oklahoma, Colorado, Kansas, and Nebraska	Buchannan and Talmage (1954); Udvardy (1969); Humphrey (1974); Meaney et al. (1987)
Lepus alleni	Limitedly NE in Arizona	**1**; lack of records in N Cochise Co. until 1976 (Allen 1895, Roth and Cockrum 1976)
Sciurus aberti	NW in Colorado, N into Wyoming, W into Utah	Davis and Bissell (1989); known dispersal ability and history of ponderosa pine distribution (Davis and Brown 1989)
Baiomys taylori	N from SE Texas into Oklahoma, and NE in New Mexico	Diersing (1979); Stangl and Dalquest (1986); Taylor and Davis (1947) vs. Davis (1974); recent record in Luna Co., New Mexico (W. Gannon, personal communication); Choate et al. (1990)
Sigmodon hispidus	N in the U.S.; through Kansas to Nebraska, and N in Rio Grande Valley in New Mexico	Cockrum (1952); Mohlenrich (1961); Jones (1960); Cameron and Spencer (1981)
Sigmodon fulviventer	N in New Mexico	Mohlenrich (1961)
Sigmodon ochrognathus	NW in Arizona and N in Texas	Davis and Dunford (1987); Davis and Ward (1988); Davis et al. (1988); Hollander et al. (1990); Stangl and Dalquest (1991)
Microtus mexicanus	Various in Arizona; N in New Mexico into S Colorado	This study
Nasua nasua	NW in Arizona and perhaps in New Mexico	Not reported by early explorers (Davis 1982); not recorded in Arizona until 1892, in extreme S (Hoffmeister 1986); no late Pleistocene record (Harris 1985, Tabor 1940); Wallmo and Gallizioli (1954); but see Kaufmann et al. (1976)
onepatus mesoleucus	NW in Arizona	**1**; recent records (Hoffmeister 1986)
ayassu tajacu	N in Arizona and New Mexico	Indian name for peccary is of Spanish origin (Sowls 1984); rarely encountered by early explorers (Davis 1982); no use by early prehistoric cultures (Crosswhite 1984, Sowls 1984)

1938, and others prior to 1975, found no Mexican voles near Cimarron, New Mexico, although other vole species were taken (Armstrong 1972, Findley et al. 1975). The Mexican vole is now common in the area (Finley et al. 1986); thus, the northward range expansion by this species may be continuing into northeast New Mexico and southeast Colorado.

Discussion and Conclusions

The historical legacy hypothesis requires widespread late Pleistocene distribution. The fossil record documents the late Pleistocene presence of *Microtus mexicanus* in southern New Mexico, adjacent portions of Texas, and (perhaps) southeast Arizona. Despite the admittedly weak fossil record, however, there is no evidence that the species' range formerly included the entire area where populations now exist (Harris 1985). Several lines of evidence support post-Pleistocene dispersal for this species:

1. Distance as a predictor of presence/absence (Lomolino et al. 1989).
2. The close relationship of adjacent Arizona populations, isolated by theoretically crossable habitat.
3. Its presence in isolated habitats unlikely to have served as post-Pleistocene refugia.
4. Recent records suggesting dispersal in northwest and northeast Arizona, central and northeast New Mexico, and southern Colorado.

Although the distribution of the Mexican vole undoubtedly has been influenced by historical events and by local extinctions, it is difficult to ignore the evidence of past and continuing post-Pleistocene dispersal.

A reviewer of this paper asked why the Mexican vole and other small mammals took 4000 years to reach certain localities that we claim were colonized within the past few decades. This point requires clarification. First, there have been local changes in vegetation and climate in the Southwest during the past 50 to 100 years, and these conditions may have favored recent dispersal even though the broader picture has remained constant for some 4000 years. Second, we do not claim that these recent records represent the *first* colonizations by the Mexican vole or other species. They are simply the first such events that have been recorded in the literature. If these animals were able to cross unsuitable habitat once, then they could have done so repeatedly in the course of centuries.

Our suggestion of recent dispersal by the Mexican vole should be evaluated in the context of a more general pattern involving many mammal species. Post-Pleistocene dispersal has influenced montane species assemblages throughout much of the Southwest (Lomolino et al. 1989). In addition, we propose a second pattern of recent northward range expansion involving at least 19 North American mammal species, all primarily austral in distribution but occupying a wide range of habitats (Table 1).

This pattern of northward dispersal is not easily explained, and there is unlikely to be a single causative factor. For some species, the shift appears to result from climatic change and/or habitat modification by humans. Alternatively, the pattern can be viewed as one small, recognizable northward surge in a continuing Holocene cycle of north/south distribution shifts.

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CAN TOWNSEND'S GROUND SQUIRRELS SURVIVE ON A DIET OF EXOTIC ANNUALS?

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ABSTRACT.—Southwestern Idaho desert shrub–bunchgrass rangeland is being invaded by fire-prone exotic annuals that permanently dominate the landscape following wildfires. This study was undertaken to describe diets of Townsend's ground squirrels (*Spermophilus townsendii idahoensis*) at four study sites with varying degrees of exotic annual invasion to determine if the squirrels could utilize high proportions of exotic annuals in their diets. Townsend's ground squirrels were collected in March and May of 1987 and 1988, and stomach contents were analyzed using a microhistological technique. Grasses comprised 37–87% of Townsend's ground squirrel diets at the four sites. Native species, especially Sandberg's bluegrass (*Poa secunda*), winterfat (*Ceratoides lanata*), big sagebrush (*Artemisia tridentata*) and six-weeks fescue (*Vulpia octoflora*) constituted 7–96% ($\bar{x}$ = 47.2%) of the diet, whereas exotic species, especially cheatgrass (*Bromus tectorum*), tumbleweed (*Salsola iberica*), and tansymustards (*Descurainia* spp.) made up 4–68% ($\bar{x}$ = 48.0%) of the diet. At each site 2–4 species comprised >90% of the diet. There was no apparent correlation between the importance values of exotic species at a site and their importance in Townsend's ground squirrel diets.

Key words: Spermophilus townsendii, *food habits, dietary analysis, Idaho, ground squirrels.*

The Snake River Birds of Prey Area is a 243,000-ha tract of multiple-use shrub-steppe rangeland administered by the U.S. Bureau of Land Management. Townsend's ground squirrels (*Spermophilus townsendii idahoensis*) are important prey of raptors, and continued existence of the area's dense breeding populations of raptors depends upon dense Townsend's ground squirrel populations (U.S. Department of Interior 1979).

Invasion of southwestern Idaho rangeland by exotic annuals such as cheatgrass (*Bromus tectorum*), tumblemustard (*Sisymbrium altissimum*), pinnate tansymustard (*Descurainia pinnata*), and tumbleweed (*Salsola iberica*) has resulted in frequent and destructive wildfires that kill native shrubs and weaken native bunchgrasses. Over time, fires have resulted in the permanent replacement of native shrub- and bunchgrass-dominated communities by exotic annual-dominated communities (Yensen 1980, Kochert and Pellant 1986).

Townsend's ground squirrel populations are much less stable in exotic annual-dominated commmunities than in native shrub communities (Yensen et al. 1992). Native perennial forbs, bunchgrasses, and shrubs apparently provide a more constant, stable food source than exotic annual species that may vary in productivity between wet and dry years by several orders of magnitude (Young et al. 1987).

Like other ground squirrels of subgenus *Spermophilus*, Townsend's ground squirrels eat green vegetation early in their four- to five-month active season, then eat seeds of grasses and forbs to fatten up for hibernation (Howell 1938, Rickart 1982). In southwestern Idaho, Townsend's ground squirrels are in estivation/hibernation from June or July until the following January or February with low survival rates (ca. 28%; Smith and Johnson 1985). Food quantity and quality could influence overwintering survival as well as reproductive success the following spring.

Townsend's ground squirrels are known to eat native forbs (*Sphaeralcea*: Davis 1939), bunchgrasses (*Poa* sp.; June grass, *Koeleria* sp.; Davis 1939), and desert shrubs (big sagebrush, *Artemisia tridentata*; budsage, *Artemisia spinescens*; shadscale, *Atriplex confertifolia*; Davis 1939, Johnson 1961), as well as insects such as grasshoppers and cicadas, and occasionally carrion

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TABLE 1. Vegetation importance values (% relative cover plus % frequency) in May 1987 and 1988 at four study sites near Coyote Butte in the Snake River Birds of Prey Area, southwestern Idaho.

Species	Study Site							
	Big sagebrush		Native grasses		Exotic annuals		Rehabilitation seeding	
	1987	1988	1987	1988	1987	1988	1987	1988
GRASSES								
Bromus tectorum	25	2	11	33	86	35	0	31
Poa secunda	67	60	90	58	45	45	85	60
Vulpia octoflora	16	7	24	0	2	8	12	3
Sitanion hystrix	16	11	14	14	8	21	0	28
Agropyron desertorum	0	0	0	0	0	0	29	2
SHRUBS								
Ceratoides lanata	29	47	3	5	0	0	7	0
Artemisia tridentata	33	39	0	0	0	4	0	0
Atriplex nuttallii	0	0	0	0	0	0	0	20
FORBS								
[a]*Salsola iberica*	0	0	33	26	0	0	40	18
[a]*Descurainia sophia*	0	0	3	0	0	0	0	0
[a]*Sisymbrium altissimum*	0	11	8	31	34	14	0	5
[a]*Lactuca serriola*	0	0	0	0	0	0	4	0
Other forbs	0	5	0	9	0	2	0	2
TOTAL COVER (%)	35	24	26	15	21	10	18	14

[a]Exotic species

(Howell 1938, Alcorn 1940). However, they do eat introduced cheatgrass, tumblemustard, peppergrass (*Lepidium perfoliatum*; Davis 1939) as well as crop species like alfalfa, wheat, barley, potatoes, beets, carrots, and lettuce (Howell 1938).

Johnson (1980) and Rogers and Gano (1980) studied diets of *Spermophilus townsendii townsendii* in Washington and found native bluegrass (*Poa* sp., 26–29%) and lupine (*Lupinus laxiflorus*, 11–25%) to be dietarily important, whereas *Descurainia* was the only exotic eaten in quantity (15–33%); cheatgrass, tumbleweed, tumblemustard, and peppergrass constituted 0–4% of the diet. Johnson et al. (1977) estimated the percent volume of food categories in 174 Townsend's ground squirrel stomachs in the Snake River Birds of Prey Area. They found grasses, including cheatgrass, were most important, followed by forbs and winterfat (*Ceratoides lanata*).

Because cheatgrass, tumbleweed, tumblemustard, and peppergrass are becoming increasingly dominant in the Snake River Birds of Prey Area, this study was designed to learn if Townsend's ground squirrels were substituting these exotics for native species in their diets. We also wished to learn if consumption-introduced plant species increased with increases in the proportion of exotic annual species in the habitat. However, the study was not designed to study dietary preference as such.

STUDY SITES

Four study sites were located near Coyote Butte, approximately 19 km south of Kuna, Ada County, Idaho, in the Snake River Birds of Prey Area. The sites described below were selected for progressively greater deviation from undisturbed native vegetation.

UNBURNED BIG SAGEBRUSH.—This site (T1S, R1W, Sec. 24; elev. 850 m) is a big sagebrush–winterfat mosaic and represents the unburned condition of the other three sites. Big sagebrush, winterfat, and native grasses (Sandberg's bluegrass [*Poa secunda*], squirreltail [*Sitanion hystrix*], and six-weeks fescue [*Vulpia octoflora*]) dominate the site; cheatgrass is the main exotic annual (Table 1).

NATIVE GRASS.—This site (T1S, R1W, Sec. 13; elev. 850 m) is <1 km northwest of the unburned big sagebrush site in a former big sagebrush–winterfat community burned by a human-caused wildfire on 26 August 1983. The fire killed the shrubs, and the site was dominated subsequently by native Sandberg's bluegrass, six-weeks fescue, and squirreltail, with some introduced tumbleweed, cheatgrass, and other exotic annuals present (Table 1).

EXOTIC ANNUALS.—This site (T1S, R1W, Sec. 13; elev. 850 m) is adjacent to the native grass site and was similar to it prior to the 1983 burn (D. L. Quinney, unpublished data). Both sites were burned by the same fire. However, since the fire, the exotic annuals cheatgrass and tumble mustard, with some remnant native grasses, especially Sandberg's bluegrass (Table 1), have dominated the site.

REHABILITATION SEEDING.—This site is located 6 km east, 2.5 km south (T1S, R1E, Sec. 27; elev. 885 m) of the unburned big sagebrush site. The area burned in 1981, was reseeded with desert wheatgrass (*Agropyron desertorum*) in 1982, but burned again in 1983. In 1987 and 1988, the area was dominated by Sandberg's bluegrass, desert wheatgrass, tumbleweed, and other native and exotic forbs (Table 1).

METHODS

To determine the degree of exotic annual invasion at each site, vegetation analysis was conducted in early June 1987 and late May 1988 while Townsend's ground squirrels were being collected. At each site we used a transect with forty 1-m^2 quadrats spaced at 10-m intervals (Daubenmire 1959). Percent cover of each species was estimated using a 1-m^2 quadrat frame divided into tenths to facilitate estimation. To give a better approximation of the availability of each plant species, percent relative cover and percent relative frequency were converted to importance values (Cox 1990).

Squirrels were collected by trapping and shooting at all four sites in May and June 1987 ($n = 75$) and in March and May 1988 ($n = 42$) except from the rehabilitation seeding site in May 1988. Squirrels were aged in the field using pelage and body weight criteria (Bureau of Land Management, unpublished data). Representative specimens were prepared as (1) standard study skins with skulls ($n = 12$), (2) skeletons ($n = 3$), or (3) skulls only ($n = 25$) and deposited in the Albertson College Museum of Natural History. Tooth-wear patterns (Yensen 1991) were consistent with the age assignments for all specimens. Based on these criteria, all 1987 specimens were juveniles since they were collected late in the active season while the adults were entering seasonal torpor; all 1988 specimens were either yearlings or adults.

Stomachs were removed from the animals immediately postmortem and preserved in 70% ethanol. In the lab, stomach contents were removed from ethanol, diluted 50% with water, and homogenized 1 min in a Waring blender to produce fragments of uniform size. The homogenate was washed through a 1-mm sieve (Hansen 1978) and collected in a 0.1-mm screen to remove tiny, unidentifiable fragments. The material was then mounted on microscope slides using Hertwig's and Hoyer's media (Sparks and Malechek 1968).

Plant species in the diet were identified by comparisons to a reference collection of microscope slides using microhistological characters. All reference slides were made from catalogued specimens in the Albertson College Harold M. Tucker Herbarium and were prepared using the technique described above.

For food habits analysis, one slide was examined per stomach. Occurrence of food categories (frequency) was recorded from each of 20 microscope fields per slide using a phase-contrast microscope at 100X. Frequency/20 fields was then converted to percent relative density (Sparks and Malechek 1968) using a table developed for frequency-to-density conversion (Fracker and Brischle 1944).

The importance of each dietary category was calculated in three ways: (1) percent relative density, a standard dry-weight conversion from frequency data (Sparks and Malechek 1968); (2) percent frequency in stomachs, the percentage of stomachs from a site with the item; and (3) percent frequency in microscopic fields, the percentage of all microscopic fields from a site with the item.

Twenty microscopic fields were examined from each slide using a predetermined pattern, and frequency of occurrence of each species was recorded. The frequency of each dietary category/20 fields on one slide was compared with other slides (or replicate counts of the same slide) using the Kulczynski Index (Oosting 1956) (also well known as the Bray-Curtis similarity index [Bray and Curtis 1957])

$$2w/(a+b)$$

The index was calculated as a dissimilarity index,

$$1-[2w/(a+b)]$$

using a BASIC microcomputer program provided by Ludwig and Reynolds (1988).

Weather data were from the National Oceanic and Atmospheric Administration monthly

TABLE 2. Late season (25 May–19 June) 1987 Townsend's ground squirrel diets. Data are from stomachs of juvenile TGS at four sites in the Snake River Birds of Prey Area. Adults were entering torpor and none were collected during this period. Dietary composition is given as percent relative density (RD), percent frequency in microscope fields (MF), and percent frequency in stomachs (PS) for each dietary category. Other symbols: + = <1%, – = absent, and n = number of stomachs.

	Unburned big sagebrush			Native grasses			Exotic annuals			Rehabilitation seeding		
Dietary category	RD	MF	PS	RD	MF	PS	RD	MF	PS	RD	MF	PS
n		21			20			15			19	
GRASSES												
Bromus tectorum	22	41	71	62	93	100	31	45	87	57	74	95
Poa secunda	24	35	86	+	2	25	7	8	40	+	+	11
Sitanion hystrix	+	2	10	–	–	–	+	+	13	–	–	–
Oryzopsis hymenoides	–	–	–	+	+	5	–	–	–	–	–	–
Grass seed	+	5	19	+	1	5	+	1	13	–	–	–
Grass root?	2	9	10	+	2	5	+	3	13	–	–	–
Total grasses	49			64			39			57		
SHRUBS												
Ceratoides lanata	3	9	52	4	5	10	43	59	67	11	17	32
Artemisia tridentata	+	2	14	1	3	10	6	19	67	+	2	5
Atriplex nuttallii	–	–	–	+	+	5	2	5	13	4	12	37
Chrysothamnus viscidiflorus	–	–	–	–	–	–	–	–	–	+	2	5
Total shrubs	3			5			51			16		
FORBS												
Salsola iberica	39	69	91	3	+	40	1	3	20	7	17	63
Sisymbrium altissimum	+	+	5	5	19	60	–	–	–	2	5	21
Descurainia—2 spp.	+	2	24	+	+	5	–	–	–	–	–	–
Lepidium perfoliatum	–	–	–	2	6	20	+	1	13	1	3	21
Cryptantha interrupta	+	+	5	–	–	–	–	–	–	–	–	–
Ranunculus testiculatus	+	1	5	–	–	–	–	–	–	–	–	–
Lactuca serriola	–	–	–	1	5	25	–	–	–	2	4	5
Chenopodiaceae	–	–	–	+	+	5	+	+	7	+	2	21
Unidentified forb	–	–	–	–	–	–	–	–	–	6	7	11
Total forbs	40			11			2			18		
MISCELLANEOUS												
Insects	8	17	62	19	44	90	7	21	87	3	11	53
Fungi	–	–	–	1	4	10	+	1	7	+	2	5
Unknown	+	+	5	–	–	–	+	4	7	4	5	5
Unidentified seed	+	1	5	+	+	5	–	–	–	–	–	–
Total miscellaneous	8			20			8			8		

Idaho Climatological Data reports for the Kuna 2 NNE weather station ca. 20 km N of the study sites.

RESULTS

Vegetation Analysis

The vegetation at each site (Table 1) varied significantly from the other sites (all $p < .01$; R × C G-tests of independence; Sokal and Rohlf 1981). Using the Kulczynski Index, the similarity among the four sites averaged 48.7% (range 27–73%) in 1987. The unburned sagebrush site was more similar (60%) to the native grass site and less similar to the exotic annual and seeding sites (44 and 47%, respectively).

The vegetation at each of the four sites varied significantly (all $p < .01$; R × C G-tests of independence) between years (Table 1). Importance values averaged 65% similar (range 48–77%) at a site between years. Total percent cover decreased on all sites in 1988. In 1988, when there was less herbaceous cover, the sites were slightly more similar (x = 61.3%, range 47–74%). Thus, each site differed almost as much between years as the sites differed among each other in a given year.

Stomach Analyses

Although the three measures of dietary importance (percent relative density [=percent dry weight], percent frequency in microscope fields, percent frequency in stomachs) gave different numerical results, the rank orders among categories were generally consistent (Tables 2–4). However, percent frequency in stomachs was very sensitive to sample sizes.

There were 1–9 food categories per stomach. Site means varied from 3.8 to 4.4 categories per stomach. The total number of food categories used by all Townsend's ground squirrels sampled at a site varied from 4 to 17 on the three sampling occasions (May–June 1987, March 1988, May 1988). However, if species used in trace amounts (<5% relative density) are eliminated, only 3–6 ($\bar{x}$ = 4.0) categories were used per site and only 2–4 species comprised >10% of the diet. Species comprising >10% of the diet at one or more study sites included Sandberg's bluegrass, cheatgrass, six-weeks fescue, winterfat, big sagebrush, tumbleweed, *Descurainia* spp., seeds of bur-buttercup (*Ranunculus testiculatus*), and insects.

Grasses were important constituents of the diet in both 1987 and 1988 and often comprised over 50% of the diet (37–88% relative density, Tables 2–4). Sandberg's bluegrass and cheatgrass were both heavily utilized, especially in March 1988 (55–87% of diet). Late in the Townsend's ground squirrel active season (May and June) use of grasses declined (except at the exotic annual site in 1988). Most of the grass eaten in May–June consisted of seeds, especially of cheatgrass. Sandberg's bluegrass leaves were utilized slightly more than cheatgrass leaves (Tables 2–4), and the two together were far more important than all other grasses combined. Squirreltail was little used, although it was the third most abundant grass.

Winterfat (0–43% relative density) and big sagebrush (0–21%) were both eaten, and winterfat was especially important at the exotic site where it was least abundant. Winterfat was utilized at all sites in 1987, even though it was not abundant enough to be sampled by the vegetation analysis at the exotic annual site. In 1988 it was eaten only at the unburned big sagebrush–winterfat site, and its use declined between March and May 1988 (Table 2). Big sagebrush was used in March at all sites in both years but was less important in May.

Tumbleweed and tumblemustard were the most important forb species consumed. Tansymustards (*Descurainia sophia* and *D. pinnata*), peppergrass, seeds of bur-buttercup, and leaves of prickly lettuce (*Lactuca serriola*) were of secondary importance. All of these are introduced annuals. Bristly cryptantha (*Cryptantha interrupta*) was the only native forb found in Townsend's ground squirrel stomachs. Although 1988 sample sizes were small, the importance of forbs in the diet increased in the samples between March and May 1988, while the percentage of grasses and shrubs decreased (Tables 3–4), thus suggesting large seasonal differences between March and May diets.

A surprising number of insects were eaten, especially in May–June 1987 (3–19%; Table 2). However, insects were not important in 1988 (trace amounts at the big sagebrush site only). Insect remains were so fragmentary that identification was not usually possible. However, abundant Lepidoptera larvae could be recognized by the soft exoskeleton and prolegs, and fragments recognizable as beetle antennae and elytra were found.

The importance values of exotic species were lowest at the unburned big sagebrush site in both years and highest in the exotic annual site in 1987 and at the native grass site in 1988. However, there was no correlation between the importance values of all exotic annuals at a site and their importance in the diet at that site ($r = -.454$; Tables 1–4).

DISCUSSION

The data show that for sites with varying degrees of exotic annual invasion sampled over a two-year period, Townsend's ground squirrels can and do utilize introduced species in their diets, and that cheatgrass, tumbleweed, and tumblemustard are the most important of these.

Both the vegetation at a site and Townsend's ground squirrel diets varied considerably between years and among sites. Differences in amount of precipitation most likely account for the differences in vegetation importance values between years. There was less September–May precipitation (192 mm in 1986–87 and 170 mm in 1987–88 at Kuna ca. 20 km N). The Daubenmire quadrats were taken on the same transect in both years by the same technicians.

The substantial annual differences in Townsend's ground squirrel diets may be the result of (1) vegetation differences between years, (2) the fact that juveniles were sampled in 1987 and adults and yearlings were collected in 1988, (3) differences in collecting dates (25 May–19 June 1987 versus 16–19 May 1988), or (4) small sample sizes.

TABLE 3. Early season (March) 1988 Townsend's ground squirrel diets. Data are from stomachs of adult and yearling TGS at four sites in the Snake River Birds of Prey Area. (Juveniles were not available in March.) Dietary composition is given as percent relative density (RD), percent frequency in microscope fields (MF), and percent frequency of stomachs (PS) containing each dietary category. Other symbols: + = <1%, – = absent, *n* = number of stomachs.

	Unburned big sagebrush			Native grasses			Exotic annuals			Rehabilitation seeding		
Dietary category	RD	MF	PS	RD	MF	PS	RD	MF	PS	RD	MF	PS
n		4			5			7			16	
GRASSES												
Bromus tectorum	39	35	75	67	46	100	51	16	71	39	70	100
Poa secunda	18	73	100	16	92	100	4	86	100	39	71	100
Vulpia octoflora	+	1	25	–	–	–	–	–	–	+	+	6
Sitanion hystrix	–	–	–	–	–	–	+	+	14	–	–	–
Agropyron desertorum	–	–	–	–	–	–	–	–	–	1	1	13
Total grasses	87			83			55			79		
SHRUBS												
Ceratoides lanata	–	–	–	–	–	–	24	55	86	–	–	–
Artemisia tridentata	11	41	50	15	35	60	21	46	100	3	6	13
Atriplex nuttallii	–	–	–	–	–	–	–	–	–	3	8	19
Total shrubs	11			15			45			6		
FORBS												
Salsola iberica	–	–	–	–	–	–	–	–	–	–	–	–
Sisymbrium altissimum	–	–	–	1	5	20	+	1	14	2	4	56
Descurainia—2 spp.	2	6	25	–	–	–	–	–	–	10	25	75
Ranunculus testiculatus	–	–	–	–	–	–	–	–	–	–	–	–
Cryptantha interrupta	–	–	–	–	–	–	–	–	–	2	4	13
Halogeton glomeratus	–	–	–	–	–	–	–	–	–	1	7	13
Lepidium perfoliatum?	–	–	–	–	–	–	–	–	–	+	+	6
Crepis acuminata?	–	–	–	–	–	–	–	–	–	+	+	6
Lactuca serriola?	–	–	–	–	–	–	–	–	–	+	+	6
Chenopodiaceae	–	–	–	–	–	–	–	–	–	+	+	13
Total forbs	2			1			+			15		

The differences in age classes were probably not important. Fitch (1948) found no differences in adult and juvenile diets in California ground squirrels (*S. beecheyi*), nor did Hansen and Johnson (1976) find differences in Wyoming ground squirrel (*S. elegans*) diets by sex or age class. Dyni and Yensen (in preparation) found no dietary differences between adult/yearling and juvenile age classes in Idaho (*S. brunneus*) or Columbian (*S. columbianus*) ground squirrels. On the other hand, the 1988 data do show a strong seasonal component. Thus, the observed annual dietary differences may be a result of later collecting dates in 1987, combined with annual vegetation differences.

Although 117 stomachs were examined, the sample sizes were too small to draw many conclusions about intersite and between-season diets in 1988. This amount of collecting had a deleterious effect on local Townsend's ground squirrel densities, and we recommend use of other methods if seasonal or annual dietary shifts are of interest.

At each site, several plant species were found in Townsend's ground squirrel stomachs that did not appear in the vegetation analysis for that site. The Daubenmire (1959) method of vegetation analysis gave an intuitively acceptable estimate of dominant vegetation, but for establishing a close link between plant abundance and herbivore diets, a finer-scale method of resource analysis is necessary. Since individual Townsend's ground squirrels have large home ranges (mean = 1357 m^2; Smith and Johnson 1985) with a wide foraging radius, it is not surprising that Townsend's ground squirrels were eating species not recorded by the vegetation analysis, even though the sites were relatively homogeneous.

There was no correlation between the total abundance of exotic annuals at a site and their importance in the diet. The number of plant species in the diet not recorded by the vegetation analysis precluded determining dietary preference indices for Townsend's ground squirrels. However, examination of vegetation

TABLE 4. Late season (May) 1988 Townsend's ground squirrel diets. Data are from stomachs of adult and yearling TGS at four sites in the Snake River Birds of Prey Area. Dietary composition is given as percent relative density (RD), percent frequency in microscope fields (MF), and percent frequency of stomachs (PS) containing each dietary category. Other symbols: + = <1%, – = absent, *n* = number of stomachs. Site 1 was not sampled in 1988.

	Unburned big sagebrush			Native grasses			Exotic annuals		
Dietary category	RD	MF	PS	RD	MF	PS	RD	MF	PS
n		1			5			4	
GRASSES									
Poa secunda	2	10	100	19	40	80	–	–	–
Bromus tectorum	22	65	100	35	57	80	24	34	75
Vulpia octoflora	29	75	100	21	36	100	6	18	100
Sitanion hystrix	1	5	100	4	6	40	5	18	50
Agropyron desertorum	1	5	100	–	–	–	–	–	–
Grass seed	2	10	100	4	10	20	2	1	25
Grass root	–	–	–	5	13	60	–	–	–
Total grasses	57			88			37		
SHRUBS									
Ceratoides lanata	–	–	–	–	–	–	13	25	50
Artemisia tridentata	–	–	–	–	–	–	3	8	50
Atriplex nuttallii	3	15	100	6	14	20	2	4	25
Chrysothamnus viscidiflorus	–	–	–	–	–	–	+	1	25
Total shrubs	3			6			18		
FORBS									
Salsola iberica	22	60	100	–	–	–	–	–	–
Sisymbrium altissimum	–	–	–	6	18	60	1	4	75
Descurainia—2 spp.	–	–	–	–	–	–	15	33	50
Ranunculus testiculatus	17	55	100	–	–	–	28	43	50
Forb root	–	–	–	+	1	20	–	–	–
Total forbs	39			6			44		
MISCELLANEOUS									
Insect	–	–	–	–	–	–	+	1	25
Unknown	–	–	–	–	–	–	+	7	25
Total miscellaneous	0			0			+		

abundance (Table 1) in comparison to consumption (Tables 2–4) indicates that most of the abundant plant species were also important in the diet, and that rare plants were being used only in trace amounts. There were some interesting exceptions to this, however. Cheatgrass was dietarily important (39% relative density) but not recorded in the vegetation analysis at the rehabilitation site.

Diets became more diverse in May, probably as a result of grasses curing and seeds becoming available. Ground squirrels eat large amounts of seeds prior to entering torpor (Rickart 1982, E. Yensen, personal observation). Perhaps if insufficient seeds are available during a drought year, Townsend's ground squirrels turn to insects as a fat source. However, at the exotic annual site where insect use was highest in 1987, cheatgrass (mostly seeds) was the major constituent of the diet. This relationship should be explored further.

Although halogeton (*Halogeton glomeratus*) was not recorded by the vegetation analysis, small amounts of it were found in two stomachs at the rehabilitation site in March 1988 (Table 3). Halogeton is poisonous to livestock, but sheep can eat it with impunity in winter, probably because rains have leached the oxalates out of the dried leaves (Cook 1977). Presumably, Townsend's ground squirrels were eating dried, rather than fresh, leaves in March.

Idaho and Columbian ground squirrels have highly varied diets of 11–25 plant species per fecal pellet group (Dyni and Yensen, in preparation). However, in that study only 2–4 plant species (usually grasses) contributed >10% to the diet. Rogers and Gano (1980) found that only three plant species (*Poa* spp., *Descurainia pinnata*, and *Lupinus laxiflorus*) contributed >10% of the diet of Townsend's ground squirrels in southeastern Washington. Hansen and Ueckert (1970) found 1–5 species contributed >10% in the diverse (47 plant species) diets of

Wyoming ground squirrels in Colorado. Hansen and Johnson (1976:750) concluded that

> Richardson [=Wyoming] ground squirrels graze on a variety of plants as they fill their stomachs rather than selecting only preferred foods when their stomachs are nearly empty. This may be an evolutionary strategy developed to allow them to consume vetches. The dilution of toxic foods by non-toxic foods decreases the probability of plant poisoning.

Freeland and Janzen (1974) reviewed strategies of herbivory by mammals in response to secondary plant compounds. They suggested that a generalist herbivore should feed predominantly on one or two foods, but continue to sample other foods present. When an herbivore experiences a nutritional deficiency, it should sample all available foods until it finds something which supplies that nutrient.

The feeding strategies proposed by Freeland and Janzen (1974) and Hansen and Johnson (1976) appear to occur in several members of the subgenus *Spermophilus*. The data indicate that ground squirrels specialize on 2–4 highly nutritional species, but supplement them with a wide variety of other species, apparently as "poisoning insurance." In this study, Townsend's ground squirrels similarly depended on only a few species for the bulk of the diet, but a wide variety of trace species was not available. If any of these species should provide insufficient quantities of a key nutrient (e.g., linoleic acid necessary for hibernation), then the limited selection of food species could have negative population consequences.

The question of whether Townsend's ground squirrels can utilize exotic annuals as dietary staples is answered in the affirmative by this study. Native forb species were of minor importance in the diet, but this does not necessarily reflect preference. Native forbs are now so rare at the four sites that none were recorded by the vegetation analysis, and thus they may not have been available for consumption. Only one native forb (*Cryptantha*) was found in the stomachs. The consequences of limited dietary variety on the long-term nutrition of Townsend's ground squirrels are unknown.

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AVIFAUNA OF CENTRAL TULE VALLEY, WESTERN BONNEVILLE BASIN

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Key words: birds, avifauna, desert, aquatic habitat, Great Basin, wetlands.

Fautin (1946) described the flora and fauna of several northern desert biotic communities in Tule Valley, located 80 km west of Delta, Utah, in Millard County of western Bonneville Basin. His study during 1939 (June to September) and 1940 (April to September) included a description of greasewood (*Sarcobatus vermiculatus*) and pickleweed (*Allenrolfea occidentalis*) communities. From 1980 through 1991 while inventorying the aquatic habitats of Tule Valley, I noted the avifauna utilizing wetlands, springs, adjacent greasewood and pickleweed communities, and saline flats. This note reports on the avifauna occurring within the two communities and compares the 1980–91 faunal lisitng with that reported previously by Fautin (1946). Comparisons are also made with Fish Springs National Wildlife Refuge, located 50 km north of the Tule Valley springs. This study identifies changes in raptors and songbirds that have occurred over 40 years and notes the differences between natural springs and wetlands and those dedicated to waterfowl management.

Description of the Tule Valley Aquatic Environments

Within the greasewood and pickleweed communities of central Tule Valley are some 25 fissure-fault springs and associated wetlands. Saline flats covered in part by water from saline seepage springs occur to the east and west of these fissure-fault springs. The springs-wetlands vary in size from 100 m^2 to over 97,000 m^2 (Coyote Springs) with a total of 195,000 m^2. Conductivity of the aquatic systems varies from 1200 (spring sources) to greater than 93,000 umhos per cm (some wetlands and saline ponds). Three-cornered bulrush (*Scirpus americanus*) and salt grass (*Distichlis spicata*) are the dominant emergent species, with *Phragmites australis*, *Typha domingensis*, and *Scirpus acutus* occurring in highly localized stands. Tamarisk (*Tamarix ramosissima*) is the only shrub growing within some springs-wetlands but was not noted by Fautin (1946).

Methods

A total of 36 visits were made to Tule Valley between 1980 and 1991, with 10 visits of two-day durations occurring in 1981. Inventories were conducted during each month (except January) with emphasis during March, May, and June. Birds were inventoried by random encounters, and unidentified species were not pursued. Nomenclature follows that of Peterson (1990).

Results and Discussion

Table 1 lists the 80 species of birds identified during 1980–91, the months they were encountered, and those species also reported by Fautin (1946). Mallard (scientific names noted in Table 1), Northern Harrier, Horned Lark, Common Raven, and Marsh Wren were encountered year-round and are considered permanent residents. Almost half (31) of the species inventoried during this study were observed two or fewer times (dates included in Table 1) and are considered casual or transient visitors. The single Palm Warbler, a casual bird in Utah (Behle et al. 1985), was identified by its characteristic tail movement as previously observed by me on numerous occasions during annual migrations in the Midwest. The saline ponds west of the fissure-fault springs hosted gulls, numerous waterfowl, and shorebirds during migration.

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Fifteen species (Great Blue Heron, Turkey Vulture, Sharp-shinned Hawk, Cooper's Hawk, Swainson's Hawk, Red-tailed Hawk, Burrowing Owl, Common Nighthawk, Western Kingbird, Northern Mockingbird, Yellow Warbler, Yellow-breasted Chat, Green-tailed Towhee, Brewer's Sparrow and Lark Bunting) observed by Fautin (1946) were not encountered in this study. Burrowing Owls, while nesting in the adjacent shadscale community, were not observed in the greasewood community. The absence of raptors (in particular the Swainson's Hawk) and the Turkey Vulture ("only occasionally seen, but observed throughout the summer in one community or another," Fautin 1946: 285) could reflect the rangeland predator control programs occurring in Tule Valley since Fautin did his studies. Absence of other species mentioned above could reflect the loss of willows (*Salix exigua*) which Fautin (1946:257) had noticed as being prevalent. Most of the birds Fautin reported for the greasewood community that were not observed during the present study were considered transients by Fautin (1946).

Over 157 species with 41 permanent residents (those species that can be found in all seasons) and 54 nesting species have been reported for Fish Springs National Wildlife Refuge (U.S. Department of the Interior 1988). This contrasts sharply with the avifauna of Tule Valley, which consists of 5 permanent residents and a total of 17 summer residents. The larger number of species at Fish Springs National Wildlife Refuge probably reflects the availability of surface water, the presence of trees and buildings, and the proximity of the springs-wetlands to the mountainous Fish Springs Range. Tule Valley springs-wetlands are undeveloped and lack the man-made features. An additional factor that may contribute to the difference in avifauna constituency of Tule Valley and Fish Springs is the contribution over many years of field ornithologists at Fish Springs National Wildlife Refuge.

Two birds, Western Sandpiper and Lincoln's Sparrow, have not been reported in this region in the Latilong study (Walters and Sorenson 1983); and the Lincoln's Sparrow was not reported at Fish Springs (U.S. Department of the Interior 1988). Fish Springs and Tule Valley are in the same Latilong region, and Fish Springs observations overwhelm the Tule Valley observations within the Latilong study.

CONCLUSIONS

A listing of the avifauna for central Tule Valley is reported. Comparisons are made to the avifauna list reported by Fautin (1946) and to the species list prepared by the Fish Springs National Wildlife Refuge. Differences in species are noted and explanations are offered.

TABLE 1. Distribution of birds in the greasewood-wetland community of Tule Valley.

	Month of Year												
	J	F	M	A	M	J	J	A	S	O	N	D	Specific dates°†
PODICIPEDIDAE													
Pied-billed Grebe *Podiceps nigricollis*						x		x					8/8/81; 6/12/82
Eared Grebe *Podilymbus auritus*						x							6/20/81
ARDEIDAE													
American Bittern *Botaurus lentiginosus*									x				9/29/84
°Great Blue Heron *Ardea herodias*													
Snowy Egret *Egretta thula*						x							6/13/82
Black-crowned Night Heron *Nycticorax nycticorax*								x		x			8/18/81; 10/20/90
THRESKIORNITHIDAE													
White-faced Ibis *Plegadis chihi*								x					8/21/87; 8/23/91

TABLE 1. Continued.

	Month of Year												
	J	F	M	A	M	J	J	A	S	O	N	D	Specific dates°°
ANATIDAE													
Canada Goose *Branta canadensis*			x										3/7/87
Green-winged Teal *Anas crecca*				x									4/27/81
°Mallard *Anas platyrhynchos*		x	x	x	x	x	x	x	x	x	x	x	
Northern Pintail *Anas acuta*			x						x			x	
Cinnamon Teal *Anas cyanoptera*			x	x	x	x	x	x	x				
American Wigeon *Anas americana*			x						x				
Canvasback *Aythya valisineria*			x										3/22/82
Redhead *Aythya americana*			x	x		x							
Merganser *Mergus sp.*			x										
Ruddy Duck *Oxyura jamaicensis*			x			x				x			
CATHARTIDAE													
°Turkey Vulture *Cathartes aura*													
ACCIPITRIDAE													
°Northern Harrier *Circus cyaneus*		x	x	x	x	x	x	x	x	x	x	x	
°Sharp-shinned Hawk *Accipiter striatus*													
°Cooper's Hawk *Accipiter cooperii*													
°Swainson's Hawk *Buteo swainsoni*													
°Red-tailed Hawk *Buteo jamaicensis*													
Rough-legged Hawk *Buteo lagopus*			x										3/7/81
°Golden Eagle *Aquila chrysaetos*			x										3/20/90
°American Kestrel *Falco sparverius*									x				9/25/82;9/29/84
°Prairie Falcon *Falco mexicanus*				x	x								4/4/82; 5/11/88
RALLIDAE													
Virginia Rail *Rallus limicola*			x					x		x			
Sora *Porzana carolina*				x				x	x				
American Coot *Fulica americana*				x	x	x	x	x	x	x			
CHARADRIIDAE													
Killdeer *Charadrius vociferus*			x	x	x	x							
RECURVIROSTRIDAE													
Black-necked Stilt *Himantopus mexicanus*								x					8/21/87

TABLE 1. Continued.

	Month of Year												
	J	F	M	A	M	J	J	A	S	O	N	D	Specific dates°°
SCOLOPACIDAE													
Spotted Sandpiper *Actitis macularia*								x					8/21/87
Western Sandpiper *Calidris mauri*				x									4/20/86
Dunlin *Calidris alpina*				x									4/20/86
Common Snipe *Gallinago gallinago*			x	x	x			x	x	x	x		
LARIDAE													
Gulls *Larus sp.*			x										
COLUMBIDAE													
°Mourning Dove *Zenaida macroura*					x	x	x	x	x				
STRIGIDAE													
°Burrowing Owl *Athene cunicularia*													
CAPRIMULGIDAE													
°Common Nighthawk *Chordeiles minor*													
APODIDAE													
White-throated Swift *Aeronautes saxatalis*				x	x	x							
PICIDAE													
Northern Flicker *Colalptes auratus*										x		x	10/25/81; 12/6/81
TYRANNIDAE													
°Western Kingbird *Tyrannus verticalis*													
ALAUDIDAE													
°Horned Lark *Eremophila alpestris*		x	x	x	x	x	x	x	x	x	x	x	
HIRUNDINIDAE													
Violet-green Swallow *Tachycineta thalassina*						x		x					5/8/81; 6/13/82
°Barn Swallow *Hirundo rustica*									x				9/19/81
CORVIDAE													
°Common Raven *Corvus corax*		x	x	x	x	x	x	x	x	x	x	x	
TROGLODYTIDAE													
Marsh Wren *Cistothorus palustris*		x	x	x	x	x	x	x	x	x	x	x	
MUSCICAPIDAE													
Mountain Bluebird *Sialia currucoides*										x			8/24/81
MIMIDAE													
°Northern Mockingbird *Mimus polyglottos*													
°Sage Thrasher *Oreoscoptes montanus*						x	x	x	x				
MOTACILLIDAE													
American Pipit *Anthus rubescens*		x	x	x	x								
LANIIDAE													
°Loggerhead Shrike *Lanius ludovicianus*								x	x		x		

TABLE 1. Continued.

	Month of Year												
	J	F	M	A	M	J	J	A	S	O	N	D	Specific dates°°
STURNIDAE													
Starling *Sturnus vulgaris*		x	x										2/21/81;3/7/81
EMBERIZIDAE													
°Yellow Warbler *Dendroica petechia*													
°Yellow-rumped Warbler *Dendroica coronata*				x	x				x	x			
Palm Warbler *Dendroica palmarum*									x				9/19/81
°Common Yellowthroat *Geothlypis trichas*					x	x	x	x					
°Yellow-breasted Chat *Icteria virens*													
°Green-tailed Towhee *Pipilo chlorurus*													
American Tree Sparrow *Spizella arborea*											x	x	9/16/80; 12/6/81
°Brewer's Sparrow *Spizella breweri*													
°Vesper Sparrow *Pooecetes gramineus*									x				9/20/81
Lark sparrow *Chondestes grammacus*					x								5/2/87
°Black-throated Sparrow *Amphispiza bilineata*				x	x	x	x						
°Sage Sparrow *Amphispiza belli*		x	x	x	x	x	x						
°Lark Bunting *Calamospiza melanocorys*													
Savannah Sparrow *Passerculus sandwichensis*			x	x	x	x	x	x	x	x	x	x	
Fox Sparrow *Passerella iliaca*										x			10/20/90
°Song Sparrow *Melospiza melodia*												x	12/5/81
Lincoln's Sparrow *Melospiza lincolnii*				x									4/4/81
°White-crowned Sparrow *Zonotrichia leucophrys*				x					x				
Junco *Junco sp.*				x									
°Red-winged Blackbird *Agelaius phoeniceus*			x	x	x	x	x						
Western Meadowlark *Sturnella neglecta*			x					x	x	x	x	x	
°Yellow-headed Blackbird *Xanthocephalus xanthocephalus*				x	x	x	x		x				
°Brewer's Blackbird *Euphagus cyanocephalus*			x						x				
°Brown-headed Cowbird *Molothrus ater*				x	x	x	x	x	x				
FRINGILLIDAE													
American Goldfinch *Carduelis tristis*												x	12/6/81
PASSERIDAE													
House Sparrow *Passer domesticus*										x			10/25/81

°Identified by Fautin 1946.

°°Dates in right column are for two [illegible]

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WILDFIRE AND SOIL ORGANIC CARBON IN SAGEBRUSH–BUNCHGRASS VEGETATION

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Key words: soil organic matter, soil organic carbon, wildfire, big sagebrush, Artemisia tridentata wyomingensis, Artemisia tridentata tridentata, *bunchgrass, long-term site degradation, Oregon.*

Soil organic matter is an important component of the environment for plants, one that enhances availability of water and nutrients (Nelson and Sommers 1982), contributes to a suitable seedbed (Monsen and McArthur 1985), and enhances seedling emergence (Wood et al. 1978). In the sagebrush region of the Intermountain West, loss of organic matter due to recurring wildfire may be a mechanism of long-term site degradation, ultimately caused by excessive livestock grazing and the introduction of aggressive annual plants (West 1988). Loss of organic matter or plant cover due to fire may increase erosion and decrease infiltration, thereby decreasing seedbed quality (Monsen and McArthur 1985). Loss of organic matter may also render soils less friable and more likely to form crusts upon drying, and so increase the resistance emerging seedlings must overcome (Wood et al. 1978). On the other hand, it is conceivable that the increase of the introduced annual cheatgrass (*Bromus tectorum* L.) that may follow wildfire (West 1988) may increase soil organic matter over the long run, due to litter accumulation. Documentation of the response of soil organic matter to wildfire in the sagebrush region is limited. On relatively mesic big sagebrush (*Artemisia tridentata* Nutt.) sites, the occurrence of a single fire apparently does not decrease organic matter in the surface soil layers (Nimir and Payne 1978, Humphrey 1984). This study concerns the effect of wildfire on soil organic matter in relatively xeric big sagebrush sites (Acker 1988).

METHODS

I studied soil organic matter at two pairs of burned and adjacent unburned big sagebrush–bunchgrass stands in northern Harney County, Oregon, USA. The stands were selected along with seven other pairs for a study of post-wildfire big sagebrush–bunchgrass vegetation dynamics (Acker 1988). I selected as study stands burned and adjacent unburned areas in which at least one of four climax bunchgrass species was present (bluebunch wheatgrass, *Agropyron spicatum* [Pursh] Scribn. & Smith; Indian ricegrass, *Oryzopsis hymenoides* [R. & S.] Ricker; needle-and-thread, *Stipa comata* Trin. & Rupr.; and Thurber's needlegrass, *Stipa thurberiana* Piper) (Hironaka et al. 1983). The climate is semiarid (28.9 cm annual precipitation on average for Burns, Oregon, about 40 km north of the study area), with hot, dry summers and cold winters (Franklin and Dyrness 1973). Soils are stony and shallow over lava or welded ash deposits, and are classified as Lithic Xerollic Haplargids mixed with Lithic Torriorthents (Lindsay et al. 1969). Within pairs, the sites are similar in elevation, slope, aspect, and surface soil texture (Table 1). Other than incidental use, none of the four stands was grazed by domestic livestock during this study or over several decades (M. Armstrong, personal communication). Shrub skeletons were present on all the burned stands. Thus, prior to the recent fires, paired stands probably had similar fire histories. The initial wildfire occurred in August 1981. The stands were sampled in the early summer

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TABLE 1. Environmental, historical, and vegetation data for burned (odd numbers) and adjacent unburned (even numbers) big sagebrush–bunchgrass stands, Harney County, Oregon, USA. Soil texture determined by method of Liegel et al. (1980).

Stand number	Elev. (m)	Aspect category[a]	Slope (%)	Soil texture, top 10 cm	Dominant plant species (1985)[b]
1	1325	9	17	sandy loam	BRTE, ERFI, POSE, PHHO, ORHY
2	1325	8	12	sandy loam	ARTRW, PHHO, ASFI
3	1360	3	19	loamy sand	BRTE, STCO2, CHVI
4	1360	2	22	loamy sand	ARTRT, BRTE, CHNA

[a] 1 = SSW, 2 = S,SW, 3 = SSE,WSW, 4 = SE,W, 5 = ESE,WNW, 6 = E,NW, 7 = ENE,NNW, 8 = NE,N, 9 = NNE (based on Muir and Lotan 1985). Categories 1–4 are warm aspects; categories 5–9 are cool aspects.

[b] Plants with at least 3% cover, in descending order. ARTRT = *Artemisia tridentata* ssp. *tridentata*, ARTRW = *Artemisia tridentata* ssp. *wyomingensis*, ASFI = Astragalus filipes; BRTE = *Bromus tectorum*, CHNA = *Chrysothamnus nauseosus* ssp. *albicaulis*, CHVI = *Chrysothamnus viscidiflorus* ssp. *viscidiflorus*, ERFI = *Erigeron filifolius*, ORHY = *Oryzopsis hymenoides*, PHHO = *Phlox hoodii*, POSE = *Poa secunda*, STCO2 = Stipa comata. Voucher specimens on file at University of Wisconsin—Madison Herbarium.

TABLE 2. Comparison of organic carbon in top 10 cm of soil in burned and adjacent unburned big sagebrush–bunchgrass stands, northern Harney County, Oregon, USA. Values are mean percentages of mass of oven-dried soil (standard errors in parentheses). Standard errors were computed using each stand's variance for 1987 and the number of subsamples for the year listed (Petersen and Calvin 1986). The number of degrees of freedom for all tests is 30 (E. Nordheim, personal communication).

Year	Organic carbon		N	Result of two-tailed t test, burned vs. unburned
			Stands 1 and 2	
1985	burned:	1.19 (0.24)	3	$.4 > P > .2$, NS[a]
	unburned:	0.83 (0.23)	3	
1986	burned:	1.17 (0.21)	4	$P > .5$, NS
	unburned:	1.34 (0.20)	4	
1987	burned:	1.31 (0.10)	16	$.4 > P > .2$, NS
	unburned:	1.15 (0.10)	16	
			Stands 3 and 4	
1985	burned:	0.63 (0.17)	3	$P > .5$, NS
	unburned:	0.68 (0.16)	3	
1986	burned:	0.60 (0.15)	4	$P > .5$, NS
	unburned:	0.65 (0.14)	4	
1987[b]	burned:	0.83 (0.07)	16	$P > .5$, NS
	unburned:	0.84 (0.07)	16	

[a] Not significant

[b] Both stands 3 and 4 burned between the 1986 and 1987 samplings.

of 1985, 1986, and 1987. Stands 3 and 4 burned again in a wildfire September 1986.

I collected samples from the top 10 cm of soil, 3 samples per stand in 1985, 4 in 1986, and 16 in 1987. In the first two years sampling locations were laid out in a systematic manner. In 1987 samples were collected in a stratified random manner. The randomization for the only remaining unburned stand, stand 2, was further restricted so that the area under shrub canopies was sampled roughly in proportion to the cover of shrubs in the stand. Shrubs can influence spatial patterns of soil chemistry in big sagebrush vegetation (Doescher et al. 1984).

Organic matter of the soil samples was assessed using the Walkley-Black rapid dichromate oxidation method of organic carbon determination (Nelson and Sommers 1982). I used the standard correction factor of 1.3 to adjust for organic carbon not oxidized in the procedure. Given the uncertain quantitative relationship between soil organic carbon and soil organic matter, I report soil organic carbon, as Nelson and Sommers recommend (1982).

I used two-tailed t tests to compare organic carbon between paired stands (Sokal and Rohlf 1981). For 1985 and 1986 I used the sample variance from the 1987 observations and the sample size from the year in question to determine the denominator of the test statistic (Petersen and Calvin 1986). This was done due to the larger sample size and the (stratified) random arrangement of the 1987 samples (Greig-Smith 1983). In the strictest sense, these observations can only establish differences between adjacent stands. Applying these results to burned and unburned big sagebrush–bunchgrass stands more generally is tenuous, due to the lack of replication (Hurlbert 1984).

RESULTS AND DISCUSSION

For both pairs of stands there was no significant difference in organic carbon in the top 10 cm of soil in any of the three years (Table 2). None of the individual comparisons is suggestive of such a difference ($P > .20$ in all cases). Although I did not test statistically for a temporal trend, soil organic carbon does not appear to have changed over the course of the study in any of the stands. Thus, the recurrence of fire at stands 3 and 4 does not appear to have altered soil organic carbon.

Changes in organic matter are by no means the only ecologically important soil changes wildfire may cause in big sagebrush vegetation (e.g., increase of organic acids in burned soil; Blank and Young 1990). Furthermore, the short duration and small sample size limit the generality of conclusions. However, these stands are not unlike others in the general vicinity where climax bunchgrasses persist (Acker 1988). In addition, these stands offer a rare opportunity to observe big sagebrush–bunchgrass vegetation processes in the absence of livestock grazing.

Wildfire apparently has not decreased or increased soil organic matter on these stands. From other studies, I have concluded that post-wildfire vegetation dynamics in these stands and similar ones nearby is dominated by cheatgrass and does not feature increasing abundance of climax bunchgrasses (Acker 1988). To explain these trends may require invoking something other than irreversible site degradation, as indicated by loss of soil organic matter.

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STRUCTURE OF A WHITE-TAILED PRAIRIE DOG BURROW

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Key words: Cynomys leucurus, *burrow structure, hibernaculum, nest.*

Little published information is available on the structure of white-tailed prairie dog (*Cynomys leucurus*) burrows. Clark (1971, 1977) described the structure of two partially excavated burrows in Wyoming, and Burns et al. (1989) described structure and function of another burrow in Montana. Neither of these studies reports finding either hibernating animals or remains of known hibernators who died over winter. This note describes the structure of a burrow system in Colorado that had a known history of prairie dog use for two years prior to excavation. Burrow excavation was undertaken to establish fates of two juveniles who hibernated in the burrow in 1988 but were not resighted in 1989.

The excavated burrow is located on the Arapaho National Wildlife Refuge, Walden, Colorado (Jackson County, T8N R79W S5). Dominant shrub species include greasewood (*Sarcobatus vermiculatus*), rabbitbrush (*Chrysothamnus nauseosus*), and sagebrush (*Artemisia tridentata*). Dominant grasses are wheatgrasses (*Agropyron* spp.). The burrow system was excavated by hand in June 1989. During excavation measurements were taken periodically of depth and dimensions of tunnels and chambers.

Four entrances were located (A, B, C, and D in Fig. 1). One of these entrances had an associated mound. Remaining entrances opened into semicircular pits approximately 0.6 m in diameter. No material had been transported from below the surface or from the surrounding surface to form a crater, as constructed by black-tailed prairie dogs (*Cynomys ludovicianus*) (King 1955, Cincotta 1989). All entrances, except the mound, were filled with loose soil.

The [illegible] entrance descended from one end of an oval mound 1.5 m long, 1.2 m wide, and 0.2 m high at an angle of 70° for approximately 0.5 m and leveled off at a depth of 0.4–0.5 m. Tunnels connecting entrances measured 80–220 mm high and 80–200 mm wide and were approximately circular in cross section. These connecting tunnels were all within 0.5 m of the surface. A tunnel leading to the nest chamber descended further. Turning bays, as described by Scheffer (1937) for black-tailed prairie dogs, were found near one entrance, D (Fig. 1).

The nest chamber tunnel descended from an entrance without a mound (D in Fig. 1). A side tunnel connected to the mound. After branching, the tunnel gradually descended to a maximum depth of 1.25 m. Another branch, closer to the nest, appeared to rise and was not excavated due to time constraints. The tunnel leading to the nest chamber was 115–150 mm wide and 105–225 mm high. In front of the nest chamber were three small chambers, 190–350 mm long and 100–225 mm in diameter. One of these chambers, 350 mm before the nest chamber, contained old fecal material. Whitehead (1927) reported a feces-filled chamber in a black-tailed prairie dog burrow and suggested prairie dogs used it to avoid drowning. The present burrow system, however, had no provision to trap air if submerged (Foster 1924). Other chambers near bends in the tunnel may have permitted animals to pass one another. No stored food was found in any chambers.

An enlarged chamber was located at the end of the burrow system. This chamber had a domed ceiling, a bowl-shaped floor, and measured 210 mm high by 210 mm wide by 250 mm long. Contained within the chamber was a mass of dry, well-chewed plant material, primarily

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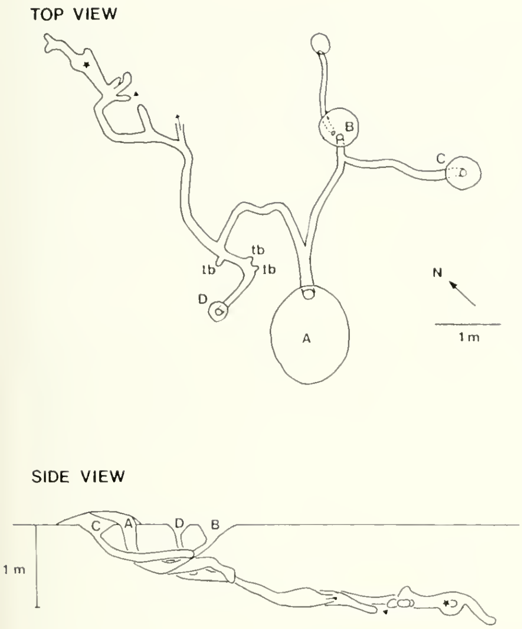

Fig. 1. Structure of excavated white-tailed prairie dog burrow. Capital letters indicate entrances to the burrow system. The nest chamber is indicated by a solid star. The location of a feces-filled chamber is indicated by a solid triangle. Turning bays are indicated by *tb*.

grasses. This was probably a nest chamber and not a food storage area because the plants found were not preferred food plants (Kelso 1939, personal observation). Several small outpocketings were found off the nest chamber. While the nest chamber and adjacent chambers and outpocketings superficially resembled a "maternity area" as described by Burns et al. (1989), this burrow had no known use as a maternity burrow in three years prior to excavation. It did, however, resemble deep, permanent systems described by Egoscue and Frank (1984).

Within the nest materials were skeletal remains and an eartag of a subadult female who hibernated in 1987 and was not resighted in 1988. Average frost depth in this area is between 500 mm and 1 m (Visher 1945), just above nest chamber depth. Juvenile males who used this burrow as a hibernaculum in 1988 were not resighted nor were their remains found.

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HYBRIDS OF WHITE-TAILED AND MULE DEER IN WESTERN WYOMING

Charles E. Kay[1,2] and Edward Boe[1,3]

Key words: white-tailed deer, mule deer, Odocoileus virginianus, Odocoileus hemionus, *interspecific hybridization, Wyoming.*

Though successful matings of captive mule deer (*Odocoileus hemionus*) and white-tailed deer (*O. virginianus*) have frequently been documented (Cowan 1962, Whitehead 1972, Day 1980, Wishart 1980), interspecific hybridization in most natural populations appears to be rare. Kramer (1973) reported only 10 hybrids out of over 17,000 deer killed in Nebraska, 2 out of 983 deer from Kansas, and only 6 out of several thousand observations in Alberta. In 34 years of fieldwork in Arizona, Knipe (1977) observed only 8 definite hybrids.

In recent years protein electrophoresis of serum albumin and restrictive endonuclease analysis of mitochondrial deoxyribonucleic acid have been used to characterize gene flow between mule and white-tailed deer populations (McClymont et al. 1982). Based on protein electrophoresis of 201 deer from 31 localities, mainly in the southwestern states, Derr (1991) found little evidence of nuclear gene introgression between the two deer species. Cronin et al. (1988) reported that mitochondrial DNA and serum albumin appeared to be distinct between mule deer and white-tailed deer throughout Montana, suggesting that interspecific gene flow was very low. This was in contrast to data from Texas that showed a 5.6% hybridization rate for 319 deer examined (Carr et al. 1986, Stubblefield et al. 1986) and Alberta where hybridization reportedly is increasing (Lingle 1989).

Though whitetail–mule deer hybrids have been observed in eastern Wyoming (Oceanak 1978), they have not been previously reported from western Wyoming. On several occasions during the winter and spring of 1990–91 we observed and photographed three female hybrid deer west of LaBarge, Wyoming, in the Green River Basin. The hybrids were always associated with female mule deer and fed with the mule deer in sagebrush (*Artemisa* spp.) habitats. The hybrids were often seen within a relatively short distance (0.5 km) of willow (*Salix* spp.) communities and hayfields along LaBarge Creek, but we never observed the hybrids keying on riparian areas, as whitetails commonly do in the arid West (Wood et al. 1989). Instead, the hybrids wintered in open sagebrush with the mule deer, where there was little hiding or thermal cover, even though temperatures of −45 C or lower are common in this part of Wyoming.

During the winter and early spring of 1991–92, we made additional observations and photographs of hybrid deer in the Green River Basin. On two separate occasions we saw a male hybrid 8 km south of Big Piney, Wyoming, in an alfalfa (*Medicago sativa*) field with approximately 100 mule deer of both sexes. We also made numerous observations of hybrids along the section of LaBarge Creek where we observed hybrids the previous year. But in 1991–92 we saw more hybrids including at least two males, four females, and three fawns. The three hybrid fawns appeared to follow a single mule deer doe and may have been triplets. These deer were usually observed with mule deer and occupied primarily nonriparian areas as the hybrids had the previous year.

Based on published characteristics and measurements (Cowan 1962, Oceanak 1978, Day 1980, Wishart 1980), the deer that we observed appeared to be first-generation hybrids. The length of the ridge on their metatarsal glands

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was intermediate between typical whitetails and typical mule deer, and the color of the metatarsal tuft was primarily white. Their tails appeared to be slightly longer than normal whitetail tails and were brown merging to black on the dorsal side and pure white on the underside. When frightened, the hybrids used a bounding gait with or without tail-flagging typical of whitetails. As reported by Lingle (1989), the hybrids did not appear to stott but used locomotion patterns intermediate between mule and white-tailed deer. On all occasions female hybrids were dominated by female mule deer they associated with and were frequently displaced from feeding sites by mule deer.

Kramer (1973:298) postulated that hybridization between mule and white-tailed deer may be more frequent where whitetails occur in very small numbers. This may be true in western Wyoming. Prior to European settlement, whitetails were apparently distributed throughout Wyoming, but unrestricted year-long meat hunting eliminated them from most of western Wyoming by the turn of the century.

> Whitetails have been in the process of either reoccupying formerly occupied areas in western Wyoming or rebuilding severely depressed populations for at least 30 years (Harry Harju, Wyoming Game and Fish Department, personal communication, 1991).

Based on hunter surveys conducted through the mail or over the telephone by the Wyoming Game and Fish Department, 85 whitetails were killed in all of western Wyoming in 1974, while 159 were killed in 1989 (Harju 1991, personal communication). Since few of these deer were checked by trained observers, there is no way of knowing how many deer reported by hunters as whitetails were actually hybrids.

In contrast, the Wyoming Range mule deer herd that winters between Big Piney and Fontenelle Reservoir, including LaBarge Creek, numbered approximately 20,000 animals after the severe winter of 1983–84. Since then, a series of seven mild winters coupled with limited doe harvest allowed this herd to increase to 55,000 in 1990 (Harju 1991, personal communication). In five years of observation we saw over 40,000 deer in the Big Piney–LaBarge Creek area, and all but a few were mule deer. One was a typical male whitetail, and the others were the hybrids described above.

Though most of these mule deer summer in the Wyoming and Salt River mountain ranges 60–100 km to the west, some reside year-long in riparian areas on LaBarge Creek and the Green River. Moreover, by the November breeding season thousands of migrating mule deer have already returned to their lower-elevation wintering areas and then commonly cross the Green River to winter in the breaks to the east. So large numbers of mule deer occupy typical whitetail riparian habitats during the rut. With the marked difference in their respective populations, it may be difficult for white-tailed deer to find appropriate mates during the breeding season. This may lead to a high hybridization rate relative to the whitetail population as appears to be the case in western Washington, where a remnant population of Columbian white-tailed deer (*O. v. leucurus*) is surrounded by a much larger population of black-tailed deer (*O. h. columbianus*) and where 18% of the whitetails tested possessed blacktail alleles at two of three diagnostic loci (Gavin and May 1988).

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WINTER NUTRIENT CONTENT AND DEER USE OF GAMBEL OAK TWIGS IN NORTH CENTRAL UTAH

Rosemary L. Pendleton[1], Fred J. Wagstaff[1], and Bruce L. Welch[1]

ABSTRACT.—We examined winter nutritional quality of current-year bud and stem tissues from burned and unburned stands of Gambel oak (*Quercus gambelii* Nutt.). Nutritional analyses were based on the amount of forage consumed by wintering mule deer. Deer use along the Utah Valley foothills averaged 6.25–10.7 cm of current-year growth. Of the tissues examined, post-fire bud tissue had the highest nutrient content, with a mean of 9.51% crude protein, 0.19% phosphorus, and 34.0% in vitro digestibility. Composite values (bud + stem) for unburned stands were slightly higher in crude protein and phosphorus and lower in digestibility than those reported in previous studies. Nutrient values from burned stands were significantly higher than those of unburned stands for all three measures. Tannin content of the burned-area regrowth was also higher. Overall forage value of Gambel oak to wintering mule deer is relatively low.

Key words: Quercus gambelii, Odocoileus hemionus, *nutrients, foraging behavior, utilization, browse, winter.*

Gambel oak (*Quercus gambelii* Nutt.) is a valuable year-round source of food and cover for many wildlife species, including deer, elk, bighorn sheep, small mammals, and a variety of birds (Reynolds et al. 1970, Harper et al. 1985, Tirmenstein 1988). Because of its abundance and location, oak is an important food source for wintering mule deer, providing up to 75% of the available winter browse along the Wasatch Front (Perry 1980). Winter use of oak varies with location, but it has been reported high in some areas along the Wasatch Front, declining in the presence of more palatable rosaceous shrubs (Smith 1952, Julander 1955). Deer use in western North America ranges from moderate to heavy throughout the year (Kufeld et al. 1973 and references therein). In winter preference trials, Smith (1950) and Smith and Hubbard (1954) ranked oak as 7th or higher out of 17 browse species based on time spent browsing and plant weight consumed.

Although important to wintering mule deer in terms of forage availability and palatability, oak ranks among the bottom in nutritional value (Smith 1957, Bunderson et al. 1986). Nutritional studies report winter oak browse as being low in essential nutrients and digestibility (Smith 1957, Kufeld et al. 1981, Meneely and Schemnitz 1981). Smith and Hubbard (1954) described oak as being well liked but of low forage quality. Currently, little information is available on the nutrient content of different portions of the plant stem or on the selection of plant parts by deer.

The effect of fire on the nutritional status of oak browse is also of some interest to land managers. Fire may provide an effective management tool for opening the canopy of the more

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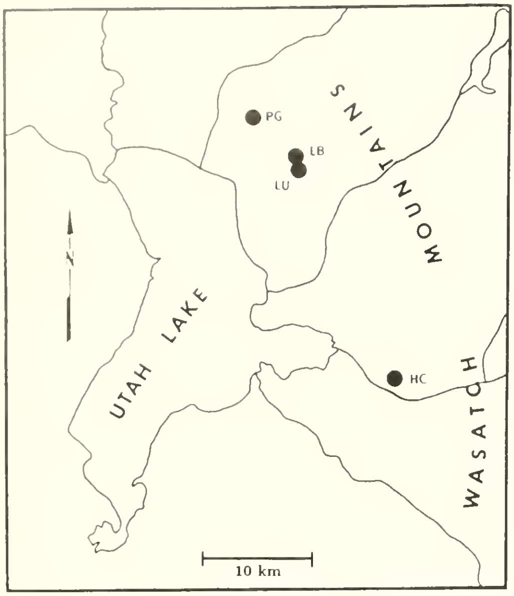

Fig. 1. Location of four oakbrush study sites in Utah County, Utah. PG = Pleasant Grove; LB = Lindon–burned; LU = Lindon–unburned; HC = Hobble Creek Canyon.

dense oak thickets to allow greater herbaceous growth (Anonymous 1966, Dills 1970, Hallisey and Wood 1976, Harper et al. 1985). Deer use of browse species has been found to increase following fire in some (Horn 1938, Hallisey and Wood 1976), but not all (Kufeld 1983), cases. The nutrient content of some oak species has been reported higher following burning (Hallisey and Wood 1976, Meneely and Schemnitz 1981).

The intent of this study was to provide a more accurate assessment of the nutrient content of oak forage consumed by wintering mule deer on the Wasatch Front. Specific objectives were (1) to determine what portion of Gambel oak twigs was used by wintering mule deer in Utah Valley, (2) to determine the percent crude protein, phosphorus, and in vitro digestibility of terminal buds and stems of Gambel oak, and (3) to compare values obtained from adjacent burned and unburned stands.

MATERIALS AND METHODS

Deer utilization was studied at locations near Lindon, Utah, above Pleasant Grove, Utah, and in the mouth of Hobble Creek Canyon (Fig. 1). Vegetation at these foothill locations consists primarily of Gambel oak and sagebrush (*Artemisia tridentata* ssp. *vaseyana*), with scattered patches of cliffrose (*Cowania stansburiana*) and bitterbrush (*Purshia tridentata*). All three locations are heavily used by wintering mule deer. In August 1987 a wildfire burned approximately 1270 acres on the southwest-facing slopes above Orem and Lindon, Utah. Oak present on the burn showed considerable regrowth two months following the fire. Two study sites were established at the Lindon location, one on the burn itself, the other in the adjacent unburned vegetation. Study sites were also established at the Pleasant Grove and Hobble Creek Canyon locations, for a total of four study sites.

Deer utilization was determined by measuring the length of marked twigs before and after browsing. In November of 1987, 679 twigs on the Lindon burn site and 660 twigs on the adjacent unburned site were marked with colored plastic tape. Twigs were selected from around the periphery of multiple clones to represent all directional aspects and a variety of heights accessible to deer. Twig lengths were measured from the tape to the end of the terminal bud. In March 1988 the twigs were remeasured and the number of centimeters browsed determined for each twig. The ratio of bud tissue and twig tissue consumed by deer was then calculated. The procedure was repeated at the Pleasant Grove and Hobble Creek sites the following year, where 186 twigs were marked and measured at each site.

Twenty-two samples for nutritional analysis were collected at mid-winter from 12 burned and 10 unburned oak clones at the Lindon location. Portions of each of the burned clones were fenced in early November to ensure availability of mid-winter collection material. In late January 200–300 stems were removed from each clone, packed in snow, and transported to the laboratory. Twigs were collected from all sides of the periphery of each clone to eliminate possible differences due to directional aspect. At the laboratory, stems from each clone sample were divided into a 1-cm terminal bud portion and an adjacent 10-cm stem. The proportion of current-year growth sampled (11 cm) was approximately equal to that removed by wintering mule deer. Where stem lengths measured less than 11 cm, total current-year growth was used in the analysis. Twig diameters at 1 and 5 cm from the tip were also recorded.

The ensuing 44 bud and stem tissue samples

TABLE 1. Summary of deer utilization on marked twigs of Gambel oak at four study sites in Utah County, Utah.

	No. twigs marked	No. twigs browsed	Percent browsed	Mean utilization (cm)[a]
Lindon–burned	679	194	28.6	10.7 ± 0.44[a]
Lindon–unburned	660	368	55.8	10.7 ± 0.24
Hobble Creek	186	112	60.2	6.3 ± 0.39
Pleasant Grove	186	157	83.9	7.7 ± 0.33

[a]Mean ± standard error

were ground using liquid nitrogen and stored at −80 C. In vitro digestibility, crude protein, and phosphorus were determined for both bud and stem portions. These three measures were considered sufficient to determine overall nutritional quality of oak as they are the nutrients most commonly deficient in winter diets of range animals (Welch et al. 1986). In vitro digestibility was assessed using Pearson's (1970) modification of the Tilley and Terry (1963) technique. This technique, while possibly overestimating in vivo digestion of cell contents in tannin-containing forages (Robbins et al. 1987, Nastis and Malechek 1988), remains the easiest and most accurate of the in vitro techniques (Nastis and Malechek 1988) and is commonly employed in nutritional studies of range forages. Inoculum for the digestion trial was obtained from a slaughter-house steer. The CO_2-injected inoculum was processed within 45 minutes of removal from the rumen (Milchunas and Baker 1982). Studies have shown that inocula obtained from domestic ruminants can successfully approximate digestibility of range forages to deer (Palmer and Cowan 1979, Welch et al. 1983). Phosphorus and crude protein determinations were made at the Plant and Soil Analysis Laboratory at Brigham Young University. Crude protein was based on Kjeldahl nitrogen content. A Technicon Auto Analyzer (Technicon Instrument Corp., Tarrytown, NY) was used to determine phosphorus content. To simplify comparisons with values reported in the literature, composite values for the complete 11-cm sample were calculated as follows: composite value = [10(twig value) + bud value]/11. Bulk samples made up of one twig from each sampled clone were tested for tannin content. Twigs were kept frozen at −80 C until use, then ground under liquid nitrogen. Tannin content for each bulk sample was determined at the Plant and Soil Analysis Laboratory using Hagerman's (1987) radial diffusion method.

Percentage data were arcsine transformed and analyzed using the General Linear Models (GLM) routine available on SAS. The model used was a 2 × 2 factorial design, with burn treatment (burned, unburned) and tissue type (bud, twig) as main effects. Clone was used as the error term for the burn treatment main effect. Tissue differences were also examined separately for burned and unburned areas because of a significant burn treatment × tissue interaction.

RESULTS

Deer use at the Lindon sites averaged 10.7 cm for both burned and unburned clones (Table 1). Individual twig use varied widely, ranging from 1.5 to 33 cm. Although mean use at the two Lindon sites was the same, the burned area had a greater proportion of small bites than the unburned area (Fig. 2). Over 24% of the bites were in the 1.5–5 cm category at the burned site as compared to 5.7% in this category at the unburned site. Also, a smaller percentage of marked twigs was browsed in the burned area (Table 1). Mean use at the Pleasant Grove and Hobble Creek sites during the milder 1988–89 winter was somewhat less than at the Lindon sites, averaging 7.7 and 6.3 cm, respectively (Table 1).

Results from the nutrient analysis of sampled tissues are given in Table 2. Main effects from the analysis of variance were all highly significant. Post-burn sprouts contained more crude protein and phosphorus and were more digestible than unburned samples. Bud tissue exceeded stem tissue in all three measures. The interaction term was also highly significant for crude protein and phosphorus ($p < .0001$ and $p = .0021$, respectively). Running separate analyses for burned and unburned areas revealed that the difference between bud and stem values was greatest for post-burn sprouts, creating the significant interaction term. Bud and

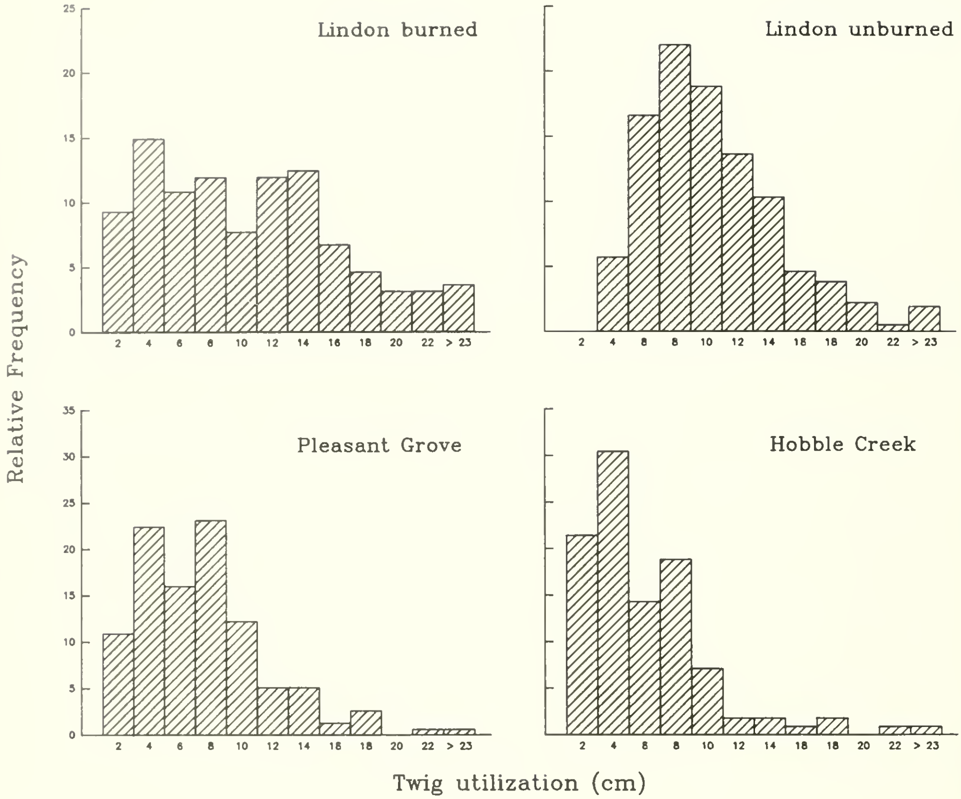

Fig. 2. Distribution of stem utilization at four oakbrush study sites in Utah County, Utah.

TABLE 2. Attained significance values from analyses of variance for nutrient content of Gambel oak.

Source of variation	Crude protein	Phosphorus	Digestibility
Burn treatment	0.0001	0.0002	0.0001
Tissue type	0.0001	0.0001	0.0001
Burn × tissue	0.0001	0.0021	0.3519
Clone	0.0001	0.0228	0.0015

twig values from burned clones differed significantly for all three variables (Table 3). Bud and twig values from unburned clones differed only in nitrogen content. Twigs from burned and unburned clones also differed in appearance, burned twigs being more slender at 1 cm (1.8 mm vs. 2.6 mm; $p = .0002$) and at 5 cm (2.1 mm vs. 2.9 mm; $p = .0001$).

Burning also had a significant effect ($p = .0001$) on tannin content. The bud tissue sample derived from burned clones had a tannin content of 4.1 mg per 100 mg plant tissue compared with 3.4 mg for unburned clones. The stem tissue sample derived from burned clones had a tannin content of 1.6 mg per 100 mg plant tissue compared with 0.7 mg for unburned clones.

DISCUSSION

Previous reports on fall-winter nutrient content of Gambel oak twigs from mature stands range from 4.6% to 5.7% for crude protein, from 0.09% to 0.10% for phosphorus (Smith 1957, Kufeld et al. 1981, Meneely and Schemnitz 1981), and from 26.6% to 40.2% for in vitro digestibility (Kufeld et al. 1981, Meneely and Schemnitz 1981). Similar values have been obtained for other oak species (Meneely and Schemnitz 1981). Composite values from unburned stands in our study (Table 2) are similar to previous results, though slightly higher in crude protein and phosphorus and slightly lower in digestibility. The use of different twig

TABLE 3. Means and standard errors for percent dry matter nutrient content of bud and twig samples collected from burned and unburned oak stands growing near Lindon, Utah. Letters following means indicate significant differences ($p = .0001$) between bud and twig values within burn treatment. Composite values = [10(twig value) + bud value]/11.

	Crude protein	Phosphorus	Digestibility
Burned stands			
Bud	9.5 ± 0.36 a	0.19 ± 0.0068 a	34.0 ± 0.59 a
Twig	7.5 ± 0.22 b	0.13 ± 0.0092 b	29.8 ± 0.70 b
Composite	7.7 ± 0.23	0.14 ± 0.0087	30.2 ± 0.66
Unburned stands			
Bud	6.5 ± 0.09 a	0.12 ± 0.0056 a	26.2 ± 1.68 a
Twig	5.7 ± 0.10 b	0.11 ± 0.0086 a	23.5 ± 1.15 a
Composite	5.8 ± 0.10	0.11 ± 0.0081	23.7 ± 1.16

lengths for nutrient analysis did not affect the overall results significantly. Composite values based on twig lengths of 7.7 or 6.3 cm (mean deer utilization at Pleasant Grove and Hobble Creek) differed very little from those based on the 11-cm sample. In the absence of foliage, buds provide the highest source of nutrients during late fall and winter. Values for leaves of Gambel oak are substantially higher in summer, but comparable to bud tissue by mid-winter (Urness et al. 1975, Meneely and Schemnitz 1981, Welch et al. 1983, Austin and Urness 1985).

Burning had a significant influence on the nutrient content of oak forage, particularly bud tissue. Values obtained from burned stands were relatively higher than those obtained from unburned stands. Post-burn bud tissue had by far the highest nutritional value of any tissues examined. Increased nutrient content of forage following fire has been reported elsewhere, although indications are that such an increase is temporary (Dills 1970, Hallisey and Wood 1976, Meneely and Schemnitz 1981, DeByle et al. 1989). The evidence to date suggests that improved phosphorus content of forage due to fire is fairly short-lived, usually lasting only one year. Nitrogen benefits may last longer, depending on the species and season. The higher values reported for burned stands in this study likely occurred because sampling took place less than one year following the burn.

Despite the slightly higher values for crude protein and phosphorus reported here for unburned stands and the markedly higher values for recently burned stands, the overall winter nutritional value of Gambel oak remains relatively low. Even post-burn bud tissue, which had the highest nutrient content of any of the tissues sampled, had a crude protein content of less than 10%. The composite value from burned clones was less than 8%, which ranks below that of sagebrush, aspen, and rosaceous shrubs (Smith 1957, Kufeld et al. 1981, DeByle et al. 1989). Actual amounts of protein digested may be somewhat less than predicted by the in vitro technique. Tannins present in summer oak and other forages have been found to increase the fecal excretion of protein by domestic livestock (Robbins et al. 1987). In mule deer and other browsers, nitrogen excretion may be reduced by tannin-binding proteins present in the saliva (Robbins et al 1987). Winter digestibility of Gambel oak is also low when compared to other forages. Bunderson et al. (1986) ranked digestibility of winter oak forage 25th out of 27 species tested. Our results are similar in digestibility to that listed in the ranking, showing slightly higher digestiblity for burned stands and lower digestibility for unburned stands.

Deer use of oak depends on many factors including cover, exposure, density of oakbrush, and availability of other forages (Smith 1952, Julander 1955, Kufeld 1983, Austin and Urness 1985). Fire affects the structure of vegetation and cover as well as quantity and quality of forage produced (Horn 1938, Hallisey and Wood 1976, Meneely and Schemnitz 1981, Kufeld 1983). Whether or not deer use an area more after burning appears to depend on structure of the oak community and type of vegetation present on adjacent areas, as well as intensity and size of burn. Where oak stands form impenetrable thickets, or where little understory is available, burning has resulted in increased use by deer (Horn 1938, Hallisey and Wood 1976). In contrast, Kufeld (1983) found increased use by elk but not deer following burning. Vegetation at this Colorado location consisted of a mixture of mature oak stands, sagebrush, snowberry (*Symphoricarpos albus*), chokecherry (*Prunus virginiana*), and serviceberry (*Amelanchier alnifolia*). Burning eliminated big sagebrush plants and decreased production of several other important browse species, partially as a result of abnormally dry weather conditions.

We found no evidence for increased use on the Lindon burned site (Table 1). The mean number of centimeters browsed at the burned site was identical to that of adjacent unburned stands, even though twigs (sprouts) from the burned stands tended to be longer. Also, a lower percentage of marked twigs was browsed at the burned site. The apparently lower use of burned twigs by deer despite higher nutrient content may be due to several factors. Oak stands in the area form discrete clones rather than large impenetrable thickets. Important browse species such as sagebrush and bitterbrush present on unburned areas were lost as a result of the fire. Also, a lack of cover and increased tannin content of forage on the burn may have had some effect on deer preference.

The oakbrush zone is critical to wintering deer populations along the Wasatch Front. Although not the most preferred winter food, its protective cover and sheer abundance make it one of the most widely used (Smith 1949, Smith and Hubbard 1954, Julander 1955). Current emphasis in the Intermountain region is to manage the oakbrush zone primarily for wildlife (Winward 1985). Several management tools have been suggested, including fire (Harper et al. 1985, Winward 1985). Burning may result in a temporary improvement in nutritional quality, as well as opening the canopy sufficiently to allow establishment of other shrub and forb species. However, without some form of follow-up treatment, the proliferation of oak sprouts may ultimately result in denser, less useable oak forage and reduction of understory species (Harper et al. 1985, Stevens and Davis 1985, Winward 1985). Moreover, the loss of fire-susceptible browse species such as big sagebrush, mountain mahogany, and bitterbrush may have serious consequences for wintering mule deer (Riggs et al. 1990), outweighing any possible benefit.

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BOTANICAL CONTENT OF BLACK-TAILED JACKRABBIT DIETS ON SEMIDESERT RANGELAND

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Abstract.—Botanical content of black-tailed jackrabbit diets was determined by microhistological examination of fecal samples collected from six different vegetation types in southern New Mexico on three dates. Grasses comprised the largest component of the jackrabbit diets, with dropseed species (*Sporobolus* spp.) and black grama (*Bouteloua eriopoda*) the most abundant grasses in the diets. Leatherweed croton (*Croton pottsii*) and silverleaf nightshade (*Solanum elaeagnifolium*) were important forbs on most vegetation types. Diet composition varied in response to season and vegetation type. Grasses were important during the summer growing season, while forbs were selected during their growing season (summer or winter-spring). Shrubs were less abundant in the diet than grasses and forbs.

Key words: microhistological analysis, fecal analysis, Lepus californicus.

Black-tailed jackrabbits (*Lepus californicus*) are widely distributed in western and central North America. They range from Canada southward to the states of Sonora and Chihuahua, Mexico, and from the Pacific coast eastward to the Great Plains (Hansen and Flinders 1969). Because of this wide distribution, jackrabbits encounter a variety of potential food sources (McAdoo and Young 1980). Considerable work has been conducted on food habits of the black-tailed jackrabbits, especially in Arizona, Colorado, and the Great Plains (Arnold 1942, Reigel 1942, Lechleitner 1958, Sparks 1968, Hansen and Flinders 1969, Flinders and Hansen 1972, Uresk 1978, Fagerstone et al. 1980, Johnson and Anderson 1984). These studies show that jackrabbits are opportunistic feeders, varying their diets depending on available forage.

In spite of the relatively large number of publications reporting the feeding habits of black-tailed jackrabbits, few have been conducted in New Mexico and the Southwest. Dabo et al. (1982) found jackrabbit diets were composed of many species, but only a few species of grasses and forbs formed the bulk of the diet. They found that diets, inferred from fecal analysis, differed among habitats for jackrabbits during summer and fall. In contrast, Fatehi et al. (1988) found similar diets among habitats on similar rangeland. The present study represents a continuation of earlier studies and should add to understanding seasonal and yearly fluctuations in diets of black-tailed jackrabbits.

STUDY AREA

The study was conducted on the New Mexico State University College Ranch about 40 km north of Las Cruces, New Mexico. The ranch lies on the Jornada Plain between the San Andres Mountains and the Rio Grande at an elevation of about 1300 m (Wood 1969, Valentine 1970). The climate of the Jornada Plain is semiarid, with a yearly mean temperature of about 16 C. Mean monthly temperatures are highest in June (35°) and lowest in January (13°). Average annual precipitation is 32 cm (range 9.2–36.2 cm), of which about 50% falls during July, August, and September (Paulsen and Ares 1962).

Fecal pellets from black-tailed jackrabbits were collected from six vegetation types (habitats): (1) mesquite (*Prosopis glandulosa*) grass, (2) snakeweed (*Gutierrezia sarothrae*), (3) mixed shrub–grass, (4) black grama, (5) creosotebush (*Larrea tridentata*), and (6) tarbush (*Flourensia cernua*). These vegetation types are characteristic of desert grassland and desert shrublands (Humphrey 1958). Major grass species include black grama (*Bouteloua eriopoda*), mesa dropseed (*Sporobolus flexuosus*), fluffgrass (*Erioneuron pulchellum*), and threeawns (*Aristida* spp.). Abundant forbs include leatherweed croton (*Croton pottsii*), wooly paperflower (*Psilostrophe tagetinae*), silverleaf nightshade (*Solanum elaeagnifolium*), and other species. Shrubs include mesquite, creosotebush, and tarbush.

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METHODS

Jackrabbit fecal material was collected from each vegetational type in June, August, and October 1988. The sample consisted of 15–20 pellets collected randomly on each date and in each of two replications of each vegetational type. Fresh pellets were identified by their shiny appearance. Field observations indicated that pellets lost their shiny appearance within a week of deposition. The pellets were dried and ground to pass through a 1.0-mm screen in a Wiley mill. The ground material was prepared as described by Bear and Hansen (1966) and Holechek (1982). Five microscopic slides were prepared from each sample, and 20 random fields were read from each slide (Holechek and Vavra 1981). Individual plant species were identified by comparison with known reference slides. All identifications were made by the senior author with an accuracy of 94%. Calculations of percent composition by weight were made following procedures outlined by Holechek and Gross (1982).

Microhistological examination of fecal material has some limitations in diet evaluations (Holechek et al. 1982). Problems are related to differential digestion of different species (Sidahmed et al. 1981), differential detection and recognition under a microscope (Westoby et al. 1976), and differential particle size reduction (Crocker 1959). In spite of these limitations, fecal analysis is one of the main methods for quantifying diet composition of wide-ranging herbivores.

Statistical analyses of dietary data were based on species counts using a split-plot, completely randomized design with vegetational type as the whole plot and sampling date as the split-plot. Differences among types, periods, and the interaction were analyzed using a categorical modeling procedure (Proc Catmod, SAS Institute 1985). Proc Catmod is a program for analyzing relative frequency data by chi-square tests.

Herbage standing crop (an estimate of herbage availability) was determined by clipping herbaceous species from ten 0.5 × 1.0-m quadrats, located randomly in each of the two replications within each vegetational type, at the time the fecal material was collected. Herbage was separated by species, oven-dried (70 C), and weighed. Shrub biomass was determined for the major species by dimension analysis as described by Ludwig et al. (1975). Preference indices were calculated as the ratio between the amount each species contributed to the diet divided by the composition in the standing crop (Krueger 1972). Only those preference indices greater than 2 are reported in this paper to indicate those species with a relatively high degree of preference.

RESULTS

Herbage Availability

Grasses contributed more than half of the herbaceous standing crop only on the black grama type (Fig. 1). Generally grass composition increased from June to August, except on the creosotebush type. Summer is the major growth period for the C_4 perennial grass species in this area (Pieper and Herbel 1982). Forbs contributed more than 50% to the plant standing crop on the mesquite-grass, black grama, and snakeweed types (Fig. 1). Shrubs were abundant (contributing about 20% of the standing crop) on the creosotebush, tarbush, and mixed shrub–grass types.

Diet Composition

Seasonal changes in jackrabbit diets appeared to be greater than standing crop availability for grasses, forbs, and shrubs (Fig. 2, Table 1). Generally, grass content of the diet peaked in August and declined until October (Fig. 2). Forb content of the diet changed little seasonally for pellets collected on the tarbush, creosotebush, and snakeweed types. Forbs comprised a larger percentage of the diet in June and October than in August on the mesquite-grass and black grama types. Shrubs generally contributed less than 25% of the diet, except for pellets collected from shrubby types at certain dates (e.g., October on the mesquite-grass type, October on the snakeweed type,

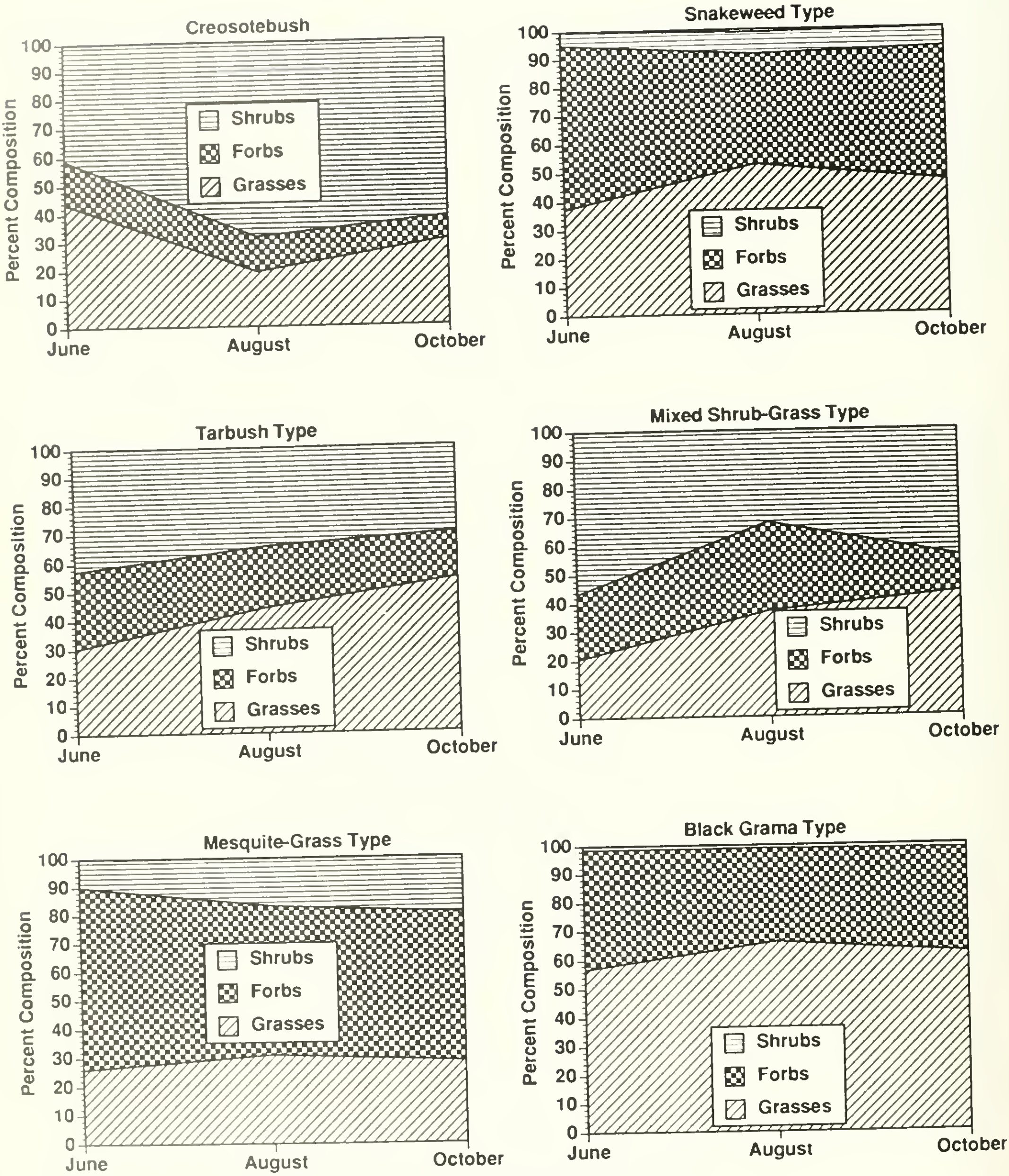

Fig. 1. Standing crop of grasses, forbs, and shrubs on different vegetation types.

June and October on the creosotebush and tarbush types).

Table 2 shows the vegetation type × date interaction was significant ($P < .05$) for several species. This interaction indicates these species did not constitute a similar percentage of the diet from June to October on the different vegetation types.

Dietary content of dropseeds varied significantly ($P < .01$) among seasons and vegetation types, and the vegetation type × date interaction was also significant (Table 2). Dropseed content of the diet was highest in pellets collected from the mixed shrub type and lowest from those collected in the tarbush type. In some types dropseed content of the diet was highest in June (e.g., mesquite-grass and snakeweed types), while in others (e.g., black grama

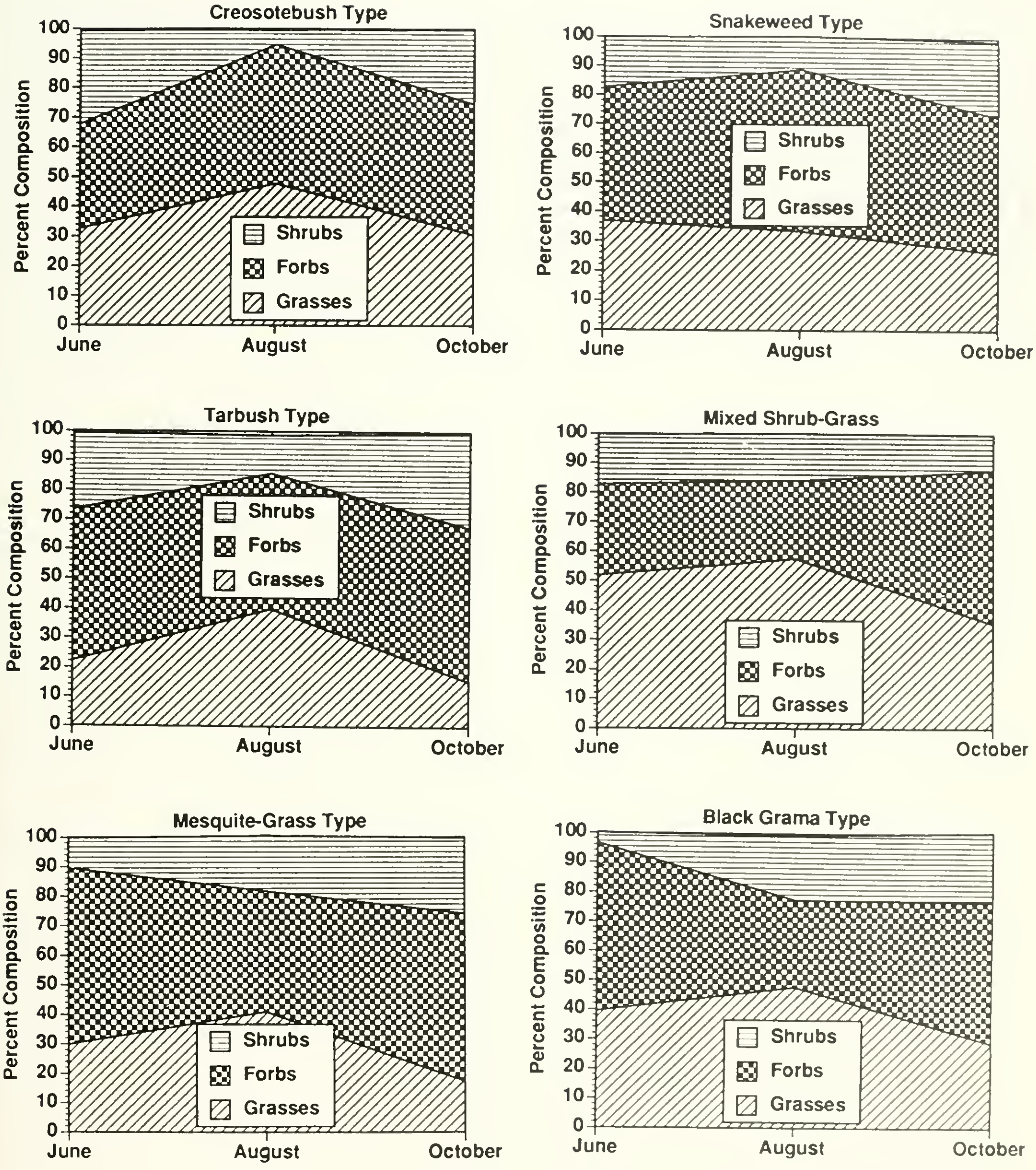

Fig. 2. Dietary content of grasses, forbs, and shrubs in pellets collected from different vegetation types.

and tarbush) it was highest in October. Dropseed content of pellets collected from the creosotebush type was consistent from June through October (Table 1).

Black grama content of pellets was not different ($P > .10$) among vegetational types, but was different among dates ($P < .10$; Table 2). In most cases black grama content of the diet peaked in August, but for some vegetational types the difference among dates was relatively small (e.g., mixed shrub type; Table 1). These inconsistencies contributed to the significant vegetational type × date interaction ($P < .01$; Table 2).

Dietary content of fluffgrass and threeawn grasses was generally low (Table 1). However, fluffgrass contributed more than 22% of the diet in June on the black grama type and more than

TABLE 1. Botanical content (%) of important plant species identified in black-tailed jackrabbit feces.

	Vegetation type																	
	Black grama			Mesquite-grass			Mixed shrub			Snakeweed			Creosotebush			Tarbush		
Species	June	August	October	June	August	October	June	August	October	June	August	October	June	August	October	June	August	October
Grasses																		
Dropseeds	9.5	9.5	17.6	20.8	12.0	10.2	26.4	24.5	17.8	12.3	9.7	10.7	15.0	15.2	17.0	2.9	0.2	9.4
Black grama	6.4	27.3	9.1	8.6	22.2	5.4	11.8	16.1	11.4	9.1	14.2	9.8	12.0	21.8	7.5	3.8	9.7	1.5
Fluffgrass	22.2	0	0.5	0	4.7	0.5	12.5	13.7	3.0	12.1	3.6	1.2	1.7	2.0	1.9	2.1	0.1	0
Threeawns	0.7	8.5	1.6	0.5	1.2	0.1	0.7	0.7	2.6	0.1	2.0	3.7	2.1	4.9	1.5	0	0	0
Total grasses	39.6	47.8	28.9	29.9	40.8	17.3	51.8	57.5	35.6	36.9	33.5	26.2	32.6	47.9	30.7	22.2	39.8	15.6
Forbs																		
Leatherweed croton	8.3	2.1	13.3	11.3	5.4	14.2	0.4	0	9.4	11.2	10.7	25.0	10.5	1.8	16.8	8.7	23.8	18.7
Dwarf dalea	9.0	0	7.3	0	2.0	0	2.8	9.5	0	0	0	0	0.3	10.3	0	9.1	0.1	0
Silverleaf nightshade	5.3	3.0	7.5	12.3	7.8	8.3	6.8	1.5	0.6	5.5	7.6	4.9	2.9	1.1	9.6	4.5	5.0	9.5
Wooly paperflower	0.3	4.1	1.6	3.3	8.0	12.9	5.1	1.5	1.2	1.1	0.9	0.6	0.6	2.8	0	0.1	1.2	0
Scarlet globemallow	0.1	0.3	2.2	5.2	8.5	4.9	1.9	0.3	13.2	3.3	10.9	1.4	6.5	2.4	5.8	6.8	4.8	8.4
Spectaclepod	4.3	2.9	0.3	0	0	0	3.0	0.1	0.1	5.4	11.1	0.1	0	0	0	0	0	0
Snakeweed	6.9	1.8	3.5	5.8	2.2	1.5	2.3	3.5	0.1	4.2	1.3	2.9	3.8	1.1	1.4	3.8	0.8	0.4
Total forbs	56.9	29.8	48.1	59.7	40.8	56.7	31.0	26.6	51.9	45.8	55.5	46.5	35.1	46.7	44.0	51.2	45.9	51.9
Shrubs																		
Mesquite	1.6	8.6	19.9	6.3	15.2	19.2	8.7	4.7	1.6	13.0	8.1	24.1	12.4	1.0	7.7	13.2	2.2	8.8
Yucca	1.1	2.8	2.4	0	1.5	2.3	6.4	8.9	1.4	0	0	0	7.2	0.4	1.3	1.6	1.8	0.5
Total shrubs	3.7	21.9	23.5	10.2	18.8	25.7	17.0	16.0	12.3	17.1	11.4	26.3	31.6	4.9	25.0	25.8	13.0	31.9

TABLE 2. Categorical analyses of botanical content of black-tailed jackrabbit diets on six vegetation types and three dates.

Grass[a]

Source	Degree of freedom	Chi-squares Ari	Boer	Mupo	Sebr	Spo	Erpu	Paob	Sele	Himu	Oth
Vegetation type	5	22.18**	65.75^{NS}	7.25^{NS}	.47^{NS}	217.41**	64.60**	.47^{NS}	8.41^{NS}	226.63**	13.96
Date	2	10.67**	142.17**	1.48^{NS}	.16^{NS}	60.37**	38.33**	.16^{NS}	2.38^{NS}	1.72^{NS}	2.92^{NS}
Type × date	10	20.70*	108.84**	30.52**	1.32^{NS}	162.54**	68.93**	1.32^{NS}	5.62^{NS}	3.88^{NS}	18.78*

[a] Ari = *Aristida* spp., Boer = *Bouteloua eriopoda*, Mupo = *Muhlenbergia porteri*, Sebr = *Scleropogon brevifolius*, Spo = *Sporobolus* spp., Erpu = *Erioneuron pulchelum*, Paob = *Panicum obtusum*, Sele = *Setaria leucopila*, Himu = *Hilaria mutica*, Oth = others.

Forbs[b]

Source	Degree of freedom	Chi-squares Bamu	Gusa	Pena	Dana	Eri	Lefe	Hyro	Crpo	Saib	Soel	Spsu	Psta	Diwi
Vegetation type	5	8.01^{NS}	35.82**	11.74*	19.53**	13.50*	25.81**	41.98**	187.86**	3.37^{NS}	72.38**	54.10**	11.23^{+}	64.71**
Date	2	43.05**	27.91**	36.90**	6.28*	2.60^{NS}	0.71^{NS}	1.57^{NS}	135.23**	1.34^{NS}	37.95**	10.64**	4.73^{NS}	9.11*
Type × date	10	17.98^{+}	38.08**	96.15**	157.31**	44.79**	35.06**	36.06**	131.23**	8.99^{NS}	121.85**	125.88**	79.51**	18.15^{NS}

[b] Bamu = *Baileya multiradiata*, Gusa = *Gutierrezia sarothrae*, Pena = *Perezia nana*, Dana = *Dalea nana*, Eri = *Eriogonum* spp., Lefe = *Lesquerella fendleria*, Hyro = *Hymenopappus robustus*, Crpo = *Croton pottsii*, Saib = *Salsola iberica*, Soel = *Solanum elaeagnifolium*, Spsu = *Sphaeralcea subhastata*, Psta = *Psilostrophe tagetina*, Diwi = *Dithyrea wislizenii*.

Shrubs[c]

Source	Degree of freedom	Chi-squares Kosp	Latr	Ziac	Eph	Atca	Prgl	Opu	Flce	Yuel	Oth
Vegetation type	5	2.11^{NS}	9.79*	11.21**	3.50^{NS}	33.88**	182.99**	23.51**	192.81**	17.19**	.90^{NS}
Date	2	.69^{NS}	12.04**	.90^{NS}	3.55^{NS}	5.51^{+}	21.32**	1.40^{NS}	.62^{NS}	14.88**	.19^{NS}
Type × date	10	6.59^{NS}	29.03**	5.12^{NS}	19.95^{NS}	23.16^{+}	359.51	32.51**	28.11**	95.72**	4.03^{NS}

[c] Kosp = *Koeberlinia spinosa*, Latr = *Larrea tridentata*, Ziac = *Zinnia acerosa*, Eph = *Ephedra* spp., Atca = *Atriplex canescens*, Prgl = *Prosopis glandulosa*, Opu = *Opuntia* spp., Flce = *Flourensia cernua*, Yuel = *Yucca elata*.

$^{+}P < .10$

$^{*}P < .05$

$^{**}P < .01$

NS = nonsignificant at .10 level

TABLE 3. Month and vegetation type when preference index exceeded 2.0 for all species in black-tailed jackrabbit diets on six vegetational types.

	Vegetational Type					
Species	Black grama	Mesquite-Grass	Mixed Shrub–Grass	Snakeweed	Creosotebush	Tarbush
Dropseed	June		June		Oct.	
Black grama		June, Aug., Oct.	Aug.	Oct.		
Fluffgrass	June, Oct.	Oct.		June	June	June
Abert's buckwheat				Oct.	June, Aug., Oct.	Aug.
Snakeweed						June
Desert baileya			Oct.			
Desert holly		Aug.	June, Oct.	Aug., Oct.	Oct.	
Dwarf dalea	Oct.					
Fendler's bladderpod	Aug., Oct.		June	June		
Globemallow		Aug., Oct.	Aug.		June, Oct.	June, Aug.
Hymenopappus		June				
Leatherweed croton		June, Aug.	Aug., Oct.	June, Aug.	June, Aug.	June
Rattlesnake weed	June				Oct.	
Silverleaf nightshade		June, Aug.	Aug.	June, Aug., Oct.		June, Aug.
Spectaclepod			Oct.	Oct.		
Wooly paperflower	Oct.	June, Oct.	June	June		
Mesquite		June		Aug.		
Yucca					June, Aug.	

12% in June and August on the mixed shrub type, and in June on the snakeweed type (Table 1). Threeawns contributed less than 9% of the diet on all dates and vegetational types.

Other grass species made small contributions to the diet. Plains bristlegrass (*Setaria leucopila*), vine mesquite (*Panicum obtusum*), and burrograss (*Scleropogon brevifolius*) did not differ in diets ($P > .10$) among vegetational types or dates, and the vegetational type × date interaction was not significant (Table 2).

Forb content of jackrabbit diets varied over time and vegetation type. For example, the content of leatherweed croton differed significantly ($P < .01$) among vegetation types and dates, and the vegetational type × date interaction also was significant ($P < .01$; Table 2). Its content varied from about 24% in pellets collected during August in the tarbush type to none in the mixed shrub type at the same time. Leatherweed croton appeared to be an important component of the diet on the black grama, mesquite-grass, and snakeweed types during most seasons (Table 1). Dietary content of other forbs was inconsistent among vegetational types and dates (Table 1). Russian thistle (*Salsola iberica*) was the only forb species with a nonsignificant ($P > .10$) vegetational type × date interaction (Table 2).

Shrub content of the jackrabbit diets was also inconsistent among vegetational types and dates. Mesquite contributed substantially to the diets on most vegetational types between June and October. Mesquite constituted more than 24% of the diets on the snakeweed type in October, but only 1% on the creosotebush type in August (Table 1). Yucca (*Yucca elata*) contributed more than 7% of the diet from the creosotebush type in June, but was not found in pellets collected from the snakeweed type on any date (Table 1). However, several shrubby species did not show a significant ($P > .10$) vegetational type × date interaction (crucifixion thorn [*Koeberlinia spinosa*], creosotebush, zinnia [*Zinnia acerosa*], and ephedra [*Ephedra* spp.]).

Dietary Preference

The preference index was generally below 2 for most grass species (Table 3). However, jackrabbits apparently preferred black grama on all dates in the mesquite-grass type. Fluffgrass was preferred during some months on all types, except for the mixed shrub–grass type. The preference index exceeded 2 for fluffgrass in June on four of the vegetational types.

The preference index exceeded 2 for several forb species (Table 3). Those with a preference index exceeding 2 for more than six combinations of vegetational type and dates included desert holly (*Perezia nana*), fendler bladderpod (*Lesquerella fendleri*), globemallow (*Sphaeralcea* spp.), leatherweed croton, and silverleaf nightshade. Dwarf dalea (*Dalea nana*) was preferred only in October in the black grama type. Dabo et al. (1982) found dalea was highly preferred and comprised as much as 65% of the diets in the fall on grassland vegetational types. Mesquite and yucca showed a preference index above 2 for June and August on three vegetational types (Table 3).

DISCUSSION

Black-tailed jackrabbits in southern New Mexico appear to be opportunistic feeders. Although this study and earlier ones indicate that as many as 30 plant species can be found in fecal samples at any one time, 5 or 6 species generally made up the bulk of the diet. Forbs often contribute a greater proportion of the diet than grasses, but the important forb species vary considerably among locations, seasons, and years. Leatherweed croton is perhaps the mainstay of the diet among the forbs, although several others, such as silverleaf nightshade and wooly paperflower (*Psilostrophe tagetinae*), contribute substantial amounts to the diets.

Dropseed, black grama, and fluffgrass appear to be the major grass species. Contrary to cattle, which utilize black grama mainly during the dormant season (Rosiere et al. 1975, Rodriguez et al. 1978), jackrabbits apparently consume more black grama during the summer growing season. Consequently, high jackrabbit densities could reduce the amount of black grama available for cattle later in the year.

Mesquite appears to be the main shrubby species in the diets, although preference for mesquite was not high. Other important shrubs varied considerably over time and space.

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SPECIES OF *EIMERIA* FROM THE THIRTEEN-LINED GROUND SQUIRREL, *SPERMOPHILUS TRIDECEMLINEATUS*, FROM WYOMING

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ABSTRACT.—Five species of the coccidian genus *Eimeria* (*E. beecheyi* [prevalence = 17.9%], *E. callospermophili-morainensis* [28.6%], *E. larimerensis* [16.1%], and *E. bilamellata* [3.6%]) were recovered from 56, 13-lined ground squirrels (*Spermophilus tridicemlineatus*) collected from two sites in eastern Wyoming. Two squirrels from one site were also passing an unidentified polysporocystic coccidian. Infected squirrels were found to harbor from one to three species simultaneously. Previously these same eimerian species were found infecting sympatric populations of Wyoming ground squirrels (*Spermophilus elegans*) and white-tailed prairie dogs (*Cynomys leucurus*) at one of the sites; it is suggested that the exchange of these generalist parasite species among co-occurring sciurid hosts contributes to the consistent prevalence levels reported in Wyoming ground squirrels.

Key words: Eimeria, Spermophilus tridecemlineatus, *prevalence, polysporocystic coccidia.*

Shults et al. (1990) reported the occurrence of six species of eimerian parasites (Protozoa: Apicomplexa) in sympatric populations of Wyoming ground squirrels (*Spermophilus elegans elegans* Kennicott, 1863) and white-tailed prairie dogs (*Cynomys leucurus* Merriam, 1890) from Wyoming. Stanton et al. (1992) conducted a study of eimerian species in four Wyoming ground squirrel populations and found that most infected ground squirrels harbored two or more species and that the eimerian assemblage was present across populations and over years.

Toft (1986) recognized two classes of parasites: micro- and macroparasites. Macroparasites (e.g., helminths) tend to produce long-lasting infections and are endemic in host populations, while microparasites (protozoa, bacteria, viruses) produce short-lived infections and long-lasting immunity, resulting in oscillations of infection frequency (epidemics) within the host population. The stability for intestinal protozoans reported by Stanton et al. (1992) does not support Toft's prediction regarding microparasites. While there have been no mechanisms proposed for maintaining stability in microparasite communities, Stock and Holmes (1987) proposed that species richness of intestinal helminth communities of grebes was enhanced by reduced host specificity which allowed parasite exchange among related hosts. One important factor in maintaining the stability of eimerian assemblages is exchange of parasite species among closely related sympatric host species.

The purpose of this study was to determine which eimerian species are present in wild populations of 13-lined ground squirrels (*Spermophilus tridecemlineatus* Mitchill, 1821) and to assess the role these hosts play in maintenance of the stable eimerian guild observed in Wyoming ground squirrels.

METHODS

In 1991 we sampled 13-lined ground squirrels from two locations: (1) a native short-grass prairie/hayfield 10 km south of Laramie, Wyoming (41°12′N, 105°33′W), and (2) a native short-grass prairie/hayfield 18 km south of Gillette, Wyoming (44°17′N, 105°31′W).

At the Laramie site squirrels were live-trapped using National live-traps once a month from July to September. Over the four-day trapping period squirrels were trapped using three 60 × 42-m trapping grids with traps set every 6 m (162 total traps). Traps were set at 2000 hr and checked each morning by 0800 hr.

At the Gillette site, six 400-m transects and

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TABLE 1. Total percent infected and prevalences (hosts infected with given species/hosts examined) of eimerian species in ground-dwelling sciurid hosts at Laramie and Gillette collection sites in Wyoming (% inf = total percent infected with *Eimeria*; Eibe = *E. beecheyi*; Eibi = *E. bilamellata*; Eica-mo = *E. callospermophili-morainensis*; Eila = *E. larimerensis*; and Eisp = *E. spermophili*).

Sciurid host	% inf	Eibe	Eibi	Eica-mo	Eila	Eisp
Spermophilus tridecemlineatus						
Laramie ($n = 41$)	43.9	7.3	2.4	9.6	14.6	0
Gillette ($n = 15$)	86.7	46.7	6.7	80.0	20.0	0
Total ($n = 56$)	51.8	17.9	3.6	28.6	16.1	0
S. elegans[a]						
Laramie ($n = 1007$)	68.0	34.0	11.0	43.0	17.0	5.0
Cynomys leucurus[b]						
Laramie ($n = 18$)	94.0	83.0	17.0	22.0	0	0

[a] Percentages for *S. elegans* and *C. leucurus* determined by taking highest of two values for *E. callospermophili* or *E. morainensis*

[b] From Shults et al. 1990

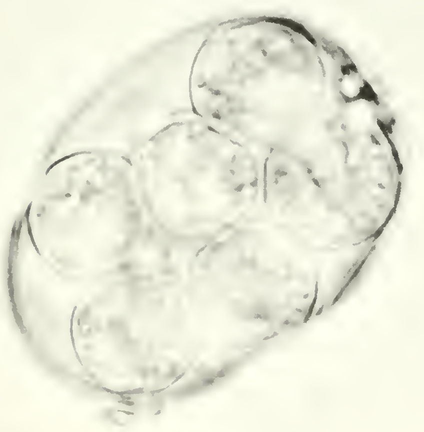

Fig. 1. Photomicrograph of a polysporocystic coccidian collected from a 13-lined ground squirrel (1250X Nomarsky interference) showing typical sporocyst with residuum clearly visible.

six 50-m transects in various vegetation types were trapped during the second week in August (3870 trap-nights). Stations were 15 m apart, each consisting of one Victor rat trap, two Victor mouse traps, and one Sherman live-trap. Sherman traps remained closed during daylight hours, and traps were checked and reset at dawn and dusk.

All fecal samples collected from animals at both sites were placed in 2% potassium dichromate solution at room temperature (25 C) for at least three weeks to allow oocyst sporulation for species identification. Oocysts were isolated by flotation in saturated sucrose solution (specific gravity = 1.2) and identified at 100X objective with an Olympus (CH) microscope. Identification to species in most cases could be accomplished based on oocyst size and external and internal morphology. However, for *Eimeria callospermophili* Henry, 1932 and *E. morainenesis* Torbett et al. 1982, the respective size ranges overlap making identification dependent on internal morphology. Unfortunately, rarely do all oocysts in a fecal sample sporulate. Therefore, although both species were identified, the two are combined into a single species complex, *E. callospermophili-morainensis*.

Comparisons of total percent infected and prevalences of each species between the two sites were made using chi-square tests (Number Cruncher Statistical System version 5.03; Hintze 1990).

RESULTS

Forty-one 13-lined ground squirrels were sampled at the Laramie site and 15 at the Gillette site. Five species of *Eimeria* were found infecting squirrels in both populations. Overall, 51.8% of all squirrels examined were infected with at least one species of *Eimeria*. The total percent infected was significantly higher at the Gillette (86.7%) than at the Laramie site (43.9%; $P \leq .05$). Infected squirrels at Gillette also had higher parasite species richness (1.77 species/infected squirrel) than at Laramie (1.17). Total percent infected and prevalences by species at each site are presented in Table 1.

Overall, the *Eimeria callospermophili-morainensis* complex was the most prevalent species found, infecting 28.6% of the 56 hosts examined. Significantly more hosts were infected with this species complex at the Gillette than the Laramie site (80% vs. 9.6%; $P \leq .05$).

Eimeria beecheyi Henry, 1932 was the second most prevalent species found, infecting 17.9% of the hosts examined. Significantly more hosts were infected at the Gillette site (46.7% vs. 7.3%; $P \leq .05$).

Eimeria larimerensis Vetterling, 1964 was found infecting 16.1% of the squirrels examined. Prevalence was higher at the Gillette site (20% vs. 14.6%), but the difference was not significant ($P \leq .05$).

Eimeria bilamellata was the least common species found during the study (3.6%). Again, prevalence was higher at the Gillette site (6.7% vs. 2.4%), but the difference was not significant ($P \leq .05$).

Two squirrels at the Laramie site were also infected with a subspherical polysporocystic coccidian (Fig. 1) with 10–12 sporocysts. The number of sporozoites could not be determined due to the large amount of residuum present in the sporocysts. Mean size for 15 measured oocysts was $38.62 \times 30.20\ \mu$. Sporocysts were spherical and measured $10.65 \times 10.65\ \mu$ ($n = 15$) and had no steida body. Both oocysts and sporocysts contained numerous residual bodies. Attempts to infect two captive Wyoming ground squirrels (*Spermophilus elegans*) were unsuccessful.

DISCUSSION

The occurrence of *E. beecheyi*, *E. bilamellata*, and *E. morainensis* in 13-lined ground squirrels constitutes new host records for these species in this host. Polysporocystic oocysts have not been previously reported from sciurid rodents. Levine et al. (1955) identified two polysporocystic species, *Klossia perplexens* from deer mice (*Peromyscus maniculatus*) and *K. variabilis* from the western big eared bat (*Corynorhinus rafinesquii*) collected at the Grand Canyon, Arizona. Because all species of *Klossia* previously described were found in invertebrates, Levine et al. (1955) postulated that the two species were parasites of invertebrates eaten by the deer mouse and bat. Dorney (1965) reported finding two polysporocystic oocysts in feces from a woodchuck (*Marmota monax*) from Pennsylvania that resembled the descriptions of the two species in the genus *Klossia* reported by Levine et al. (1955). Dorney speculated that the two oocysts might represent spurious infections of invertebrate origin. Based on these reports, it is likely that the polysporocystic coccidian observed in 13-lined squirrels is a member of the genus *Klossia* and possibly of invertebrate origin. However, identification to species requires further work, including the identification of the primary host.

The results of this study indicate that while the eimerian fauna of 13-lined ground squirrels is very similar to that of Wyoming ground squirrels and white-tailed prairie dogs, at the Laramie site there were some differences in the prevalences of the different parasites. Of the five species found infecting 13-lined squirrels, all have been reported previously from sympatric ground squirrels (Shults et al. 1990, Stanton et al. 1992), and all have been reported from white-tailed prairie dogs in Wyoming (Todd and Hammond 1968a, 1968b, Todd et al. 1968, Shults et al. 1990). However, at the Laramie site 13-lined squirrels were not as frequently infected and had lower prevalences than Wyoming ground squirrels for all species and lower prevalences than white-tailed prairie dogs for *E. beecheyi*, *E. callospermophili-morainensis*, and *E. bilamellata*. Values for 13-lined squirrels at the Gillette site (where no other species of sciurids were present) were more similar to those for Wyoming ground squirrels at the Laramie site (Table 1). Additionally, Wyoming ground squirrels had greater species richness than 13-lined squirrels (Stanton et al. 1992). Species richness for prairie dogs has not been reported.

Results indicate that related sympatric hosts can be infected by the same species of *Eimeria*, which may contribute to the stability of the eimerian guild.

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PLANT AGE/SIZE DISTRIBUTIONS IN BLACK SAGEBRUSH (*ARTEMISIA NOVA*): EFFECTS ON COMMUNITY STRUCTURE

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ABSTRACT.—The demography of black sagebrush (*Artemisia nova* Nelson) was investigated in the Buckskin Mountains of western Nevada to determine patterns of stand renewal in sagebrush communities currently free from wildfires. Biomass sampling was conducted to develop growth classes that reflected apparent age of the shrubs. The density of black sagebrush plants was twice that of basin big sagebrush (*A. tridentata* ssp. *tridentata* Nutt.) in adjacent communities on contrasting soils (2.2 versus 1.1 plants per m^2). Black sagebrush accumulated only 75% as much woody biomass as big sagebrush. Regression equations were developed and tested for predicting total woody biomass, current annual growth (CAG), and leaf weight of black sagebrush plants. Apparent age classes were developed both for the black sagebrush plants and the sub-canopy mounds on which they grew. Discriminant analysis was used to test this classification system. Plant succession, apparently controlled by nitrate content of the surface soil, appeared to eliminate the successful establishment of black sagebrush seedlings on the mounds. After the shrubs die, the mounds eventually deflate. We propose that mounds reform around shrub seedlings; but because seedling establishment is so rare in these communities, this could not be verified.

Key words: biomass, shrub succession, desert soil formation, soil nitrate, black sagebrush, Artemisia nova.

Black sagebrush (*Artemisia nova* Nelson) is one of the dwarf sagebrush species which collectively constitute about half the sagebrush vegetation in Nevada (Beetle 1960). Black sagebrush plays a dominant role in a number of plant communities in the Great Basin (Zamora and Tueller 1973). Rarely does black sagebrush share dominance with another species of *Artemisia.* In the section Tridentate of the genus *Artemisia,* black sagebrush is perhaps the species most adapted to arid environments. Black sagebrush is closely associated with shadscale [*Atriplex confertifolia* (Torr. & Frem.) Wats.] dominated landscapes (Blaisdell and Holmgren 1984). The browse of black sagebrush is highly preferred by domestic sheep (*Ovis aries*), pronghorn (*Antilocarpa americana*), and Sage Grouse (*Centrocercus urophasianus*). From the 1890s until the late 1950s, black sagebrush plant communities in the Carson Desert of Nevada were a vital part of winter range for the domestic range sheep industry. Years of excessive browsing by sheep actually shaped the outline of black sagebrush shrub canopies; Zamora and Tueller (1973) reported they had difficulty in finding relic communities in high range condition.

Vegetation of the Buckskin Mountains of west central Nevada is characterized by black sagebrush/desert needlegrass (*Stipa speciosa* Trin. & Rupr.) plant communities. The Buckskin Mountains are located 100 km southeast of Reno, Nevada, in the rain shadow of both the Sierra Nevada and Pinenut Mountains. This is a portion of the Carson Desert in which Billings (1945) suggested that *Atriplex*-dominated salt desert shrub vegetation occurred because of atmospheric drought rather than occurrence of soluble salts in the soil. If we compare the black sagebrush communities of the Buckskin Mountains with those described in the regional study conducted by Zamora and Tueller (1973), we find that the highest-elevation, north-facing slope communities of the Buckskin Mountains correspond to the most arid communities previously described. From this we assume the black sagebrush communities in this study represent an arid extension of this type.

Only recently have occasional wildfires of any extent occurred in black sagebrush communities in western Nevada. The fires that have occurred have been associated with the recent spread of the alien annual cheatgrass (*Bromus tectorum* L.) into these arid environments (Young and Tipton 1990). Apparently for much of the twentieth century these communities have not been subject to wildfires because of lack of herbaceous vegetation to carry the fire. Because of the lack of trees to produce fire scars, it is difficult to determine whether these sites were subject to periodic burning under pristine conditions. This is in sharp contrast to basin big sagebrush communities where periodic catastrophic stand renewal by burning from wildfires has been common. The lack of catastrophic stand renewal in black sagebrush communities should be reflected in the age/size class structure of the communities.

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Our purpose was to determine the age/size distribution of black sagebrush plants to determine community structure.

MATERIALS AND METHODS

Studies were conducted from 1984 through 1988 in the Buckskin Mountains located about 100 km southeast of Reno, Nevada. The geologic features of this mountain range have been described in detail by Hudson and Oriel (1979). Vegetation and soils of the range have been mapped and related to the geologic map of the area (Lugaski and Young 1988). The plant communities used in this study were located on the Guild Mine member of the Mickey Pass tuff. This geologic unit consists of crystal-rich, moderately to poorly welded ash flow tuff (Proffett and Proffett 1976). It has been proposed that the soils (a) developed in place, (b) developed from subaerially deposited material from long-distance transportation, or (c) developed from a combination of residual and subaerially deposited material (unpublished research, ARS-USDA). The bulk of the profile is an argillic horizon, about 50 cm thick, which consists of 50% or more clay-textured material. It is proposed that this clay horizon is a relic of a soil that developed on the site and whose original surface horizon has been removed by erosion. The important point is that the clay horizon, which is intermittently exposed on the soil surface, developed under different environmental conditions from the current surface horizon. The current surface soil consists of a relatively recently deposited layer, apparently from subaerial deposition, that is largely confined to mini-mounds beneath the canopies of the black sagebrush plants. The soil is classified as a fine, iridic, montmorillonitic, Typic Paleargid.

Spatial structure of the black sagebrush communities was determined by sampling five stands located along the western flank of the Buckskin Mountains. The five stands, located on the same outcropping of Mickey Pass tuff, were separated by small canyons where the westerly tilted ash flows were broken by faulting. All sites were west facing and located in a band along the mountainside at 1720–1780-m elevation.

A starting point was located on aerial photographs in each stand, and 10 plots, each 10 m^2 in area, were located randomly along line transects parallel to the slope. A total of 50 plots were established (5 stands × 10 plots per stand). In each plot the following were determined: (a) shrub density by species, (b) crown cover of shrubs (ocular estimate), (c) shrub height, (d) area of mound and interspaces, and (e) herbaceous cover (ocular estimate). Mound cover refers to the slightly raised areas beneath shrub canopies where subaerially deposited soil and saltation deposits accumulate.

At each plot location the herbaceous vegetation frequency was sampled with 100 step points arranged in 4 lines of 25 points each following the procedures of Evans and Love (1957). The herbaceous vegetation was resampled annually.

Using the same starting point, but by placing the transects up and down the slope, 25 black sagebrush mounds were located in each stand. The shrubs rooted on each mound were measured for (a) height, (b) maximum and minimum crown diameter, (c) stem number (as black sagebrush ages the cambium splits, forming multiple-stemmed plants), and (d) stem diameter at the soil surface (diameter of the group of split stems). The aerial portion of the plant was subdivided by clipping into the following categories: (a) coarse stems, 2.5 cm or larger in diameter; (b) fine stems, 0.25 to 2.4 cm in diameter; (c) current annual growth; and (d) leaves. The material was dried at 80 degrees C for 24 hours and weighed.

After the aerial portion of the shrub was removed, the litter beneath the canopy was collected and screened through a 2-mm screen. The material too coarse to pass through the screen was saved, dried, and weighed. The maximum and minimum diameters of the mound were measured, and the height of the mound was determined by digging to the clay horizon. The number of perennial grasses rooted on the mound was counted by species, and the cover of cheatgrass was estimated ocularly per mound.

A series of age/size classes was established for the black sagebrush plants sampled. These

TABLE 1. Mean plus standard error (SE) for shrub density per m^2, percent projected canopy cover, frequency (10-m^2 plot) within stands (N = 10), and constancy among stands (N = 5).

Species	Density (m^2)	SE	Cover (%)	SE	Frequency (%)	SE	Constancy (%)	SE
Artemisia nova	2.2	0.40	22	2.4	100	0	100	0
Chrysothamnus viscidiflorus	0.7	0.10	2	0.4	40	8	80	8
Ephreda nevadensis	0.3	0.08	1	0.4	64	10	100	0
Tetradymia glabrata	0.2	0.04	–[a]	–	32	5	60	4
Eriogonum microthecum	0.1	0.04	–[a]	–	5	1	20	2
Eriogonum umbellatum	0.2	0.00	–[a]	–	8	1	20	1

[a] Indicates less than 1% average cover

classes were based on the size, growth form, percentage dead canopy, and apparent age of the plants. The classes were (a) seedling, (b) young plant, (c) mature plant, (d) patriarch, (e) senescent, and (f) dead.

Soil samples from the surface 5 cm were taken (a) next to the shrub stem, (b) at the canopy edge, and (c) 10 cm beyond the edge of the shrub canopy. These samples were dried, screened, and shipped to a commercial laboratory for nitrate nitrogen analysis.

A two-way analysis of variance and post hoc Duncan's Multiple Range test were performed to analyze differences in soil nitrate concentration between sagebrush age/size classes and sample location. A series of stepwise regressions was performed, utilizing the general linear model, wherein a subset of variables was chosen that would best predict plant weight, annual growth of plant (weight), and leaf weight of black sagebrush. Separate step-up regressions were performed for plant and mound characteristics (Neter and Wasserman 1974). The independent variables that were significant contributors to predicting age/size classes for these two groups were chosen as discriminant variables to be used in two separate discriminant analyses. The age/size classes of the sagebrush plants were used as the grouping structure in the discriminant analysis. The plant characteristic variables selected as significant contributors to classification into age/size classes were (a) weight of coarse stems, (b) number of stems, (c) plant height, and (d) plant diameter. The mound characteristics (ranked in order of importance) used were (a) litter cover, (b) litter weight, (c) soil nitrate concentration, and (d) cheatgrass cover on the mound.

RESULTS AND DISCUSSION

Community Competition

The plant communities of the Buckskin Mountains dominated by black sagebrush are low in diversity (Table 1). Green rabbitbrush [*Chrysothamnus viscidiflorus* (Hook.) Nutt.] occurs in patches in the community. Nevada ephedra (*Ephedra nevadensis* Wats.) is rather evenly distributed through the black sagebrush communities, but at a low density. Littleleaf horsebrush (*Tetradymia glabrata* Gray) is a relatively infrequent component of the communities. The two species of *Eriogonum* are semiwoody species that also occurred in the most arid black sagebrush communities that Zamora and Tueller (1973) reported.

Squirreltail (*Elymus hystrix* Scribn.) and cheatgrass are the most frequent herbaceous species (Table 2). The relative frequency of the two species reverses from year to year depending on available moisture for plant growth. Cheatgrass is abundant only in years with adequate moisture during the spring. The density of squirreltail plants remains relatively constant. In dry years, squirreltail is virtually the only herbaceous species in these communities.

Biomass

Along the western margin of the Buckskin Mountains, black and basin big sagebrush communities occur side by side on sharply contrasting soils. The basin big sagebrush communities have been burned in wildfires, based on historic records and fire scar analysis (Young et al. 1989). Our analysis of black sagebrush communities is essentially based on aboveground woody material accumulation of the dominant shrub. We had previously conducted a study of the biomass

TABLE 2. Mean plus standard error (SE) for frequency of herbaceous species for an average of four years' sampling (average precipitation 175 mm), for a dry spring (1989, no April precipitation), and a year with above-average moisture available for plant growth (1986, 225 mm precipitation). Based on 5000 sample points per year.

	Frequency					
	Average		Dry (1989)		Wet (1986)	
	Four years	SE	Spring	SE	Spring	SE
Growth from species	%					
Perennial grass						
Elymus hystrix	39	4.1	70	6.9	6	0.5
Stipa speciosa	3	0.3	8	0.7	–	–
Stipa thurberiana	–[a]	–	–	–	–	–
Poa secunda	–		1	0.8	–	–
Oryzopsis hymenoides	–	–	1	0.2	–	–
Annual grass						
Bromus tectorum	44	6.6	14	2.8	76	3.8
Perennial forb						
Castilleja chromosa	1	0.2	1	0.2	–	–
Sphaeralcea parvifolia	–	–	2	0.3	–	–
Phlox hoodii	–	–	3	0.3	–	–
Annual forb						
Erodium cicutarium	5	0.8	–	–	2	0.8
Descurainia pinnata	–	–	–	–	5	0.7
Sisymbrium altissimum	5	0.9	–	–	10	0.8

[a] indicates less than 1% average cover

of basin big sagebrush adjacent to the western edge of the Buckskin Mountains (Young et al. 1989). This allowed comparison of the production of biomass of basin and black sagebrush from the same area. The basin big sagebrush community had a sandy loam surface soil and a greater soil depth (Haplargids derived from metavolcanic sources). Big sagebrush ages were clumped at 55–60, 40–45, and 10–15 years old.

The general aspect of the two communities is strikingly different, with the maximum height of the black sagebrush being 60 cm and that of the big sagebrush over 1 m. In contrast to the central woody stems of the big sagebrush plants, black sagebrush plants appear multi-stemmed. Despite the difference in height, the two communities have similar biomass because of the higher density of plants in the black sagebrush community. There is more coarse and fine woody material in the basin big sagebrush community (Table 3).

If we assume both populations are the same age (assumption is necessary because actual age of black sagebrush plants could not be estimated), the rate of woody biomass accumulation was 13.2 g/m^2/year and 64.5 g/m^2/year for black and basin big sagebrush, respectively. The wide difference between the two communities is apparently due to the higher woody biomass of more mature basin big sagebrush plants.

Woody biomass of black sagebrush was best predicted by the equation:

$$Y = 9.87 + 1.21 * X1 + 1.12 * X2 + 0.88 * X3$$

where Y = total woody biomass (grams), $X1$ = fine stems, $X2$ = coarse stems, and $X3$ = root crown. $R^2 = .96$ for this determination. Yearly growth increment was predicted by the equation:

$$Y = 16.96 + 0.26 * X1 + 0.16 * X2 - 0.73 * X3 - 0.14 * X4$$

where Y = current growth, $X1$ = fine stems, $X2$ = coarse stems, $X3$ = plant height, and $X4$ = root crown. $R^2 = .57$ for this determination, despite the inclusion of a fourth variable. Our third equation predicted leaf weight:

$$Y = 23.53 + 0.29 * X1 - 0.93 * X2 + 0.2 * X3 - 0.35 * X4$$

where Y = leaf weight, $X1$ = coarse stems, $X2$ = height of plant, $X3$ = fine stems, and $X4$ = plant density. These four variables in the equation accounted for 64% of the variability in the data.

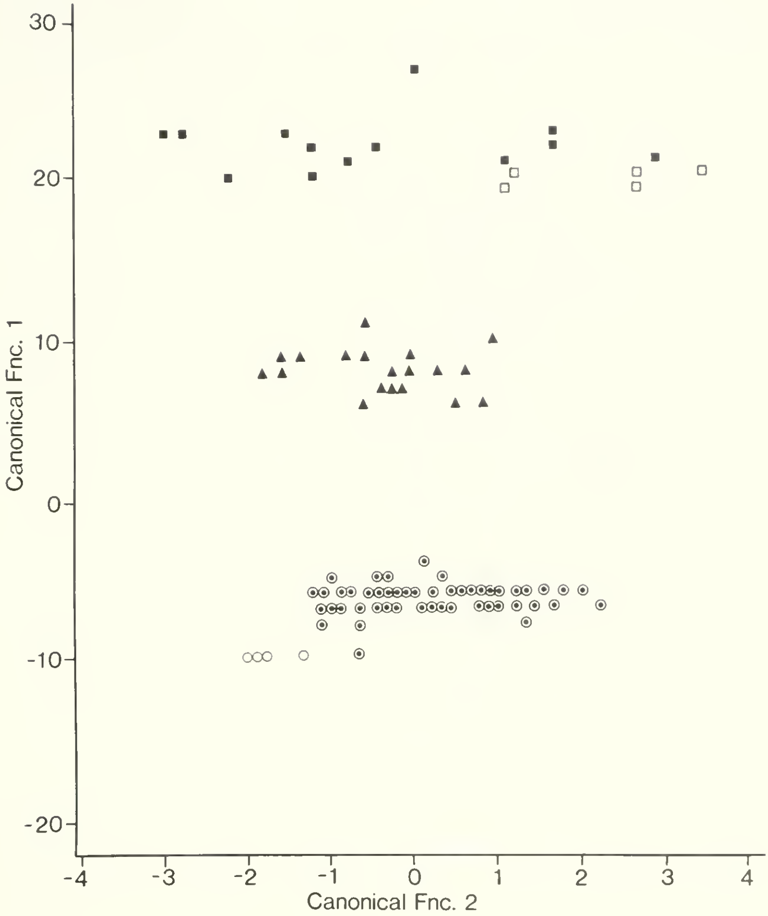

Fig. 1. Plot of black sagebrush group membership based on plant characteristic discriminant equations where ○ = young ⦿ = mature, ▲ = patriarch, ■ = senescent, and □ = dead.

Age/Size Classes

The selected variables for both plant and mound characteristics were important contributors in distinguishing between age/size classes and were good indicators of group composition (Fig. 1). Very few misclassifications occurred by use of the resulting discriminant functions.

The bulk of the black sagebrush stands was composed of mature plants 20–60 cm tall with canopies 20–50 cm in diameter (Table 4). This is a wide range in height and canopy size, but the mature age/size class was distinguished from young plants by the presence of up to 10% dead material in the canopy and the beginning of the separation of the stem into individual cambium bundles. The patriarch class was distinguished from the mature class by an increase in dead material in the canopy (to 30%) and complete separation of the stems. The separated stems formed U-shaped flutes with the open end of the U toward the former center of the stem. It was not possible to establish the maximum age of the class because the center of the stem was missing. The individual section had at least 40 growth rings.

Senescent plants formed the next, apparently older, age/size class. In this class at least 50% of the canopy was dead. Older black sagebrush plants do not get taller, probably because they have no central stem to support the canopy. The diameter of the crowns does increase. There is a marked increase in woody biomass between the patriarch and senescent classes.

Seedlings and young plants constituted only 6% of the black sagebrush populations (Table 4).

TABLE 3. Mean density (stems/m^2) plus standard error (SE) and oven-dry biomass (g/m^2) of *Artemisia nova* and *A. tridentata* subsp. *tridentata*. Data for *A. tridentata* subsp. *tridentata* from a previous study (Young et al. 1989).

Species	Density		Biomass per m^2									
			Coarse		Fine		CAG		Leaves		Total	
	m^2	SE	g	SE	g	SE	g	SE	g	SE	g	SE
Artemisia nova	2.2	0.4	750	90	520	60	180	45	130	40	1550	240
Artemisia tridentata subsp. *tridentata*	1.1	0.3	850	100	970	110	170	40	130	50	2120	420

TABLE 4. *Artemisia nova* crown and biomass characteristics for individual age/size classes. Demographic breakdown of black sagebrush communities by growth classes. Classes are related to age for younger plants, but once stems separate, ages are not based on annual rings.

	Crown characteristics				Biomass characteristics						
Age/size class	Height (cm)	Diameter (cm)	Density (%)	Dead branchlets (%)	Coarse stems (g)	Fine stems (g)	CAG (g)	Leave (g)	Stem number	Percentage of stand	Age (years)
Seedling	5	5	30	0	0	15	5	10	1	>1	2–5
Young plant	10–20	5–10	50	0	28	64	30	40	1	5	5–30
Mature	20–60	10–50	80	10	140	120	80	60	Multiple	60	30–50
Patriarch	20–60	20–80	60	30	560	420	140	100	Multiple	17	40+
Senescent	20–60	20–100	30	60	980	640	60	30	Multiple	12	?
Dead	20–60	20–100	0	100	910	320	0	0	Multiple	5	?

with seedlings being very rare. The separation between seedling and young plants was based on the occurrence of coarse, woody biomass in the latter class. Young plants had entire stems with no evidence of division of the cambium.

Mound Types

Each black sagebrush age/size class had a corresponding type of sub-canopy mound. The only seedling found in the entire study was located in an interspace between mounds. Obviously, one seedling is not a valid sample, but the lack of seedlings is a critical factor in the dynamics of the communities studied. The first detectable mound occurred under young plants. Only 5–10% of the sub-canopy area under black sagebrush plants in the young plant age/size class was covered with litter (Table 5). The litter was composed of fragments of black sagebrush leaves.

In the mature plant age/size class the cover of litter and the weight of litter increased (Table 5). The mounds were easily distinguished by both height and surface soil color and texture. The surface of the mounds appeared darker in color, and the reddish tinge to the clay surface soils of the interspace was not apparent. If the surface of the mound was disturbed, the dark color was replaced by a grayish shade. Mounds appear to reach their maximum height with this growth stage of black sagebrush. Mounds of mature plants had perennial grasses associated with the sub-canopy area. The most frequent perennial grass was squirreltail.

Litter accumulations increased with the patriarch age/size class, but height of the mound did not increase. Apparently, trapping of subaerial deposition material and saltation particles must be related to growth stage of black sagebrush plants in terms of crown architecture. Subaerially deposited particles are obviously very unstable and subject to redeposition if they fall in the largely bare interspace among shrub mounds (Young and Evans 1986). If litter accumulation increases on patriarch mounds, why do they not trap these secondary erosion products and the mound keep growing in height? Canopy structure changes with the patriarch age/size class, with increasing bare stems and spreading, but not taller, plants. It would appear that aerial dynamics of the crown of black sagebrush plants influence mound height.

With the senescent age/size class, a divergence

TABLE 5. Mound characteristics in relation to age/size classes of *Artemisia nova*. Illustrates that mound characteristics change with age/size classes of shrubs.

	Mound			Litter					
		Diameter							
Black sagebrush growth classes	Height (cm)	Max (cm)	Min (cm)	Cover (%)	Depth (cm)	Weight (g)	Perennial grass density (per mound)	Cheatgrass cover (%)	Number Samples
Seedling	0	0	0	0	0	0	0	0	1
Young plant	2–5	60	30	5–10	0.5	40	0	2	6
Mature	5–15	80	40	40–60	1–1.5	480	2.0	15	76
Patriarch	10–15	100	60	80	2–3	690	2.8	12	21
Senescent	10–15	100	60	80	2–3	720	2.1	60	15
Dead	10–15	100	60	80	2.5–5	970	6.4	5	6

TABLE 6. Mean nitrate level (mg/kg) of soil at the stem, canopy edge, and outside the canopy of black sagebrush plants in relation to maturity classes, Buckskin Mountains, Nevada.[a]

	Location[b]			
Age/size class	Stem (ppm)	Canopy (ppm)	Outside (ppm)	Age/size class mean[c]
Young plant	4.7 h	4.3 hi	4.1 hi	4.4 d
Mature	6.6 g	5.5 g	4.0 j	5.4 c
Patriarch	10.5 d	12.0 b	8.0 e	10.2 a
Senescent	13.2 a	11.3 c	7.0 f	10.5 a
Dead	8.4 c	7.0 f	7.1 f	7.5 b
Mean location[b]	8.7 a	8.0 b	6.0 c	

[a] Means followed by the same letter are not significantly different at the .01 level of probability as determined by Duncan's Multiple Range test

[b] Means of location followed by the same letter are not significantly different at the .01 level of probability as determined by Duncan's Multiple Range test

[c] Means of age/size classes followed by the same letter are not significantly different at the .01 level of probability as determined by Duncan's Multiple Range test

in herbaceous species composition on the mounds occurs (Table 5). Some mounds become densely covered with cheatgrass as black sagebrush plants become senescent and others support colonies of squirreltail.

After the black sagebrush plants die, litter weight continues to increase and litter changes in appearance. Litter under dead plants is composed of stringy bark fragments, and individual black sagebrush leaves cannot be distinguished in the litter.

Soil Nitrate Levels

Surface soil nitrate levels were higher beneath shrub canopies than in the interspace (Table 6). Levels were highest next to shrub stems. Nitrate levels beneath the canopy rose as age/size classes of black sagebrush indicated older plants and mounds. This is in itself an indication that age/size classes actually do reflect increasing age. The development of vertical and horizontal patterns in soil nitrogen, attributed to the localization of litter fall beneath the canopies of desert shrubs, has been documented by the research of N. E. West and co-workers (Charley and West 1977, West and Skujins 1977, West 1979). Nitrate levels of surface soils dropped significantly ($P \leq .01$) once the black sagebrush plants died. Nitrate levels in surface soils at the edge of shrub mounds increased with apparent increasing age of black sagebrush plants and mounds. These areas correspond to the micro-topoedaphic situation described as coppice benches by Eckert et al. (1989) for shrub mounds in big sagebrush communities. Apparently the increase in soil nitrate results from leaching from the mounds. Once black sagebrush plants are dead and grasses dominate the mound, soil nitrate levels decrease.

Mounds and Black Sagebrush Community Structure

We did not find grass-dominated mounds or grass-dominated mounds with black sagebrush seedlings. We did note the remains of mounds that appeared to be eroding away. Apparently, mounds are dynamically formed and eroded in relation to the establishment and eventual death of black sagebrush plants. The failure to find grass-dominated mounds may be a function of herbivory by domestic livestock [sheep, feral horses (*Equus caballus*), and black-tailed jackrabbits (*Lepus californicus*)]. Grass-dominated mounds may fail to persist since grasses cannot maintain mounds because of leaf fall and canopy structure differences compared with black sagebrush plants. The only patchy vegetation encountered in the communities was groups of rabbitbrush plants. Perhaps rabbitbrush increases after relatively short-lived squirreltail plants die or are reduced by grazing. In an adjacent big sagebrush community we previously determined three episodes of seedling establishment at 12, 42, and 57 years before 1985 (Young et al. 1989). Plant ages were clustered around these apparent establishment dates. The clusters may represent periods of desirable climate for seedling establishment or a single season when establishment occurred; they may also represent variability in growth ring deposition or recognition. The classes we constructed in this study are much too broad to pinpoint this type of episodic stand establishment for black sagebrush. Perhaps black sagebrush communities not renewed catastrophically by wildfires only require stand renewal at such low levels (5% of the stand, standing dead plants) that our one seedling sampled is sufficient for community regeneration.

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MUSHROOM CONSUMPTION (MYCOPHAGY) BY NORTH AMERICAN CERVIDS

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ABSTRACT—Native mushrooms play an important, though often underestimated, role in deer, elk, and caribou diets in North America. Mushrooms are often noted as an unusual or anomalous food in the diets of cervids; yet they often dominate diets in the late summer and fall in forested areas of western North America and throughout the year in the southeastern U.S. Mushrooms are particularly high in protein (16–19%), phosphorus (average 0.75%), and potassium (average 2%). Also, mushroom production is generally greatest in fall. Therefore, they are a highly nutritious food in late season when other native forages may marginally meet basal nutrient requirements of ungulates.

Key words: caribou, cervid, deer, diet, elk, mycophagy, mushroom, nutrition, ruminant.

Wildlife scientists have long recognized that certain highly nutritious, "bonus" foods frequently contribute significantly to animal welfare though their contribution (%) to the diet may be small (e.g., acorns, mushrooms, and mesquite beans). By seeking out these high-quality but generally scarce or ephemeral foods, herbivores can balance nutrients against lower-quality forages that are more abundant. Native mushrooms have often been recorded as a "bonus" food in the diets of deer, elk, and caribou in North America. However, their contribution to cervid nutrition is not commonly understood.

The term "mushroom" refers to the fleshy fruiting body (sporocarp) of many species of fungi. Mushrooms are technically not "plants." They belong to the kingdom Mycetae under the five-kingdom classification system (Whittaker 1969). The primary mushroom-producing fungi are in the group called Basidiomycetes, but many mushrooms eaten by wildlife, including morels, are Ascomycetes. Mushroom production is triggered when species-specific requirements of minimum temperature and moisture conditions are met (Smith and Weber 1980).

Mushroom consumption (mycophagy) has been recorded for many wildlife species in North America. Mushrooms are eaten by ungulates (e.g., deer and elk), small mammals (e.g., squirrels and armadillos), as well as birds, turtles, and insects (Miller and Halls 1969, Fogel and Trappe 1978, Martin 1979). Mushrooms have long been recognized as an important component of small mammal diets (Fogel and Trappe 1978). However, mushrooms are seldom considered a significant component of cervid diets even though they have been anecdotally recorded as a "preferred" food item. Discounting mushrooms as an important dietary component may stem from a misunderstanding of their nutritive value. The purposes of this review are to (1) assess the contribution of mushrooms to cervid diets, (2) summarize the known literature on the nutritive value of mushrooms to ungulates, and (3) assess the implications of mycophagy to habitat selection and nutritional ecology.

CONTRIBUTION OF MUSHROOMS TO DEER, ELK, AND CARIBOU DIETS

Mushroom Consumption by Deer

Many studies have recorded mushrooms in diets of both mule (*Odocoileus hemionus*) and white-tailed (*Odocoileus virginianus*) deer (Table 1). Diet composition estimates range from a trace to a majority of the diet. On the upper limit, 71.2% mushrooms, on a fresh-weight basis, were recorded in fall deer diets in Alabama (Kirkpatrick et al. 1969), 65.8% in August diets in Arizona (Hungerford 1970), and 59.5% in August diets in Montana (Lovaas 1958).

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TABLE 1. Proportion of mushrooms in deer, elk, and caribou diets in North America averaged over season[a].

Species	% of diet					
State or Province (Vegetation type)[b]	Spring	Summer	Fall	Winter	Kind of data[c]	Source[d]
Mule deer (*Odocoileus hemionus*)						
Colorado (spruce/fir/pine forest)	–	0.3	–	–	Obs. (% bites)	31
Montana (spruce/fir/pine forest)	0.0	12.1	0.0	0.0	Rum. (% vol.)	21
Utah (dry mountain meadow)	–	7.0	–	–	Obs. (% mass)	10
Utah (mature conifer forest)	–	15.0	–	–	Obs. (% mass)	10
Utah (stagnated conifer forest)	–	14.0	–	–	Obs. (% mass)	10
Utah (conifer forest/oak woodland)	–	5.4	9.3	–	Obs. (% mass)	4
Arizona (mixed-conifer forest)	–	16.4	–	–	Obs. (% time)	16
California (chaparral-oak woodland)	–	–	–	<1.0	Rum. (% vol.)	20
British Columbia (conifer forest)	0.0	0.0	13.0	4.0	Rum. (% vol.)	8
White-tailed deer (*Odocoileus virginianus*)						
New Brunswick (conifer/deciduous forest)	13.7	6.7	9.1	–	Rum. (% mass)	26
Maine (pine-hemlock forest)	0.0	0.0	45.0	0.0	Obs. (% mass)	9
Pennsylvania (clear-cut forest)	1.6	0.2	0.8	4.5	Obs. (% time)	14
Southeastern U.S. (oak-hickory-pine forest)	2.1	19.8	8.4	6.2	Rum. (% vol.)	12
Southeastern U.S. (mixed-pine forest)	0.4	15.6	8.6	4.9	Rum. (% vol.)	12
Southeastern U.S. (southern evergreen forest)	0.6	16.4	5.4	3.2	Rum. (% vol.)	12
Virginia (eastern deciduous forest)	0.0	40.0	2.5	0.0	Rum. (% vol.)	19
North Carolina (oak-hickory-pine forest)	0.0	10.6	7.0	0.0	Rum. (% vol.)	19
South Carolina (mixed pine forest)	0.2	33.4	2.6	10.7	Rum. (% vol.)	19
Georgia (southern evergreen forest)	0.0	9.7	9.0	13.8	Rum. (% vol.)	19
Florida (southern evergreen forest)	1.4	10.4	26.7	13.2	Rum. (% vol.)	19
Florida (southern evergreen forest)	–	–	–	9.2	Rum. (% vol.)	11
Florida (pine-scrub oak forest)	–	–	–	25.2	Rum. (% vol.)	11
Alabama (southern pine-hardwood forest)	0.0	71.2	0.5	17.4	Rum. (% vol.)	19
Alabama (southern pine-hardwood forest)	7.3	–	4.8	0.8	Rum. (% vol.)	1
Louisiana (pine-bluestem range)	0.5	1.5	3.5	<0.5	Obs. (% bites)	28
Louisiana (pine-hardwood forest)	–	0.4	1.9	0.7	Obs. (% bites)	29
Louisiana (clear-cut forest)	–	<0.1	2.1	0.2	Obs. (% bites)	29
Texas (pine-mixed hardwood forest)	3.0	34.0	1.0	7.0	Rum. (% mass)	25
Oklahoma (oak savannah)	0.0	0.0	4.3	1.0	Rum. (rel. freq.)	30
Wisconsin (northern hardwood forest)	–	2.0	–	–	Rum. (% vol.)	22
Minnesota (northern hardwood forest)	–	–	<1.0	0.0	Rum. (% vol.)	2
South Dakota (pine forest)	0.0	4.0	2.1	0.0	Rum. (% vol.)	15
South Dakota (pine forest)	–	0.7	0.5	<0.5	Rum. (% vol.)	23
Elk (*Cervus elaphus*)						
Virginia (eastern deciduous forest)	–	–	1.0	–	Rum. (% vol.)	3
Saskatchewan (pine forest)	–	5.3	–	–	Rum. (% mass)	17
Saskatchewan (mixed forest)	–	4.2	–	–	Rum. (% mass)	17
Utah (dry mountain meadow)	–	4.2	8.3	–	Obs. (% mass)	7
Utah (mature conifer forest)	–	18.7	55.7	–	Obs. (% mass)	7
Utah (stagnated forest)	–	18.4	55.4	–	Obs. (% mass)	7
California (Pacific rain forest)	–	–	0.3	–	Obs. (% time)	13
Caribou (*Rangifer tarandus*)						
Newfoundland (conifer forest)	0.0	25.0	12.0	0.0	Rum. (% vol.)	5
Northern Canada (conifer forest)	–	–	–	0.4	Rum. (% vol.)	24
Northern Canada (boreal forest)	–	1.2	–	–	Rum. (% vol.)	18
Alaska (spruce forest/tundra)	0.0	12.0	10.0	2.0	Obs. (% vol.)	6
Alaska (spruce forest)	–	–	45.0	–	Rum (% vol.)	27

[a] A dash (–) listed as % of diet means no data were available.

[b] General descriptions given by authors or vegetation area according to Aldrich 1963.

[c] Obs. = observational data; Rum. = rumen contents.

[d] Key to references: (1) Adams 1959; (2) Aldous and Smith 1938; (3) Baldwin and Patton 1938; (4) Beale and Darby 1991; (5) Bergerud 1972; (6) Boertje 1984; (7) Collins 1977; (8) Cowan 1945; (9) Crawford 1982; (10) Deschamp et al. 1979; (11) Harlow 1961; (12) Harlow and Hooper 1971; (13) Harper 1962; (14) Healy 1971; (15) Hill and Harris 1943; (16) Hungerford 1970; (17) Hunt 1979; (18) Kelsall 1968; (19) Kirkpatrick et al. 1969; (20) Leopold et al. 1951; (21) Lovaas 1958; (22) McCaffery et al. 1974; (23) Schneeweis et al. 1972; (24) Scotter 1967; (25) Short 1971; (26) Skinner and Telfer 1974; (27) Skoog 1968; (28) Thill and Martin 1986; (29) Thill et al. 1990; (30) Van Vreede 1987; (31) Wallmo et al. 1972.

Late summer and fall are generally the seasons of greatest mushroom consumption, probably because mushroom production is generally greatest then. Though mushroom biomass production is seldom recorded in diet studies, several authors note that mushroom production is triggered by fall rains (Tevis 1952, Hungerford 1970, Urness 1985).

The mushroom species most consumed by deer are not precisely known because species are seldom recorded in diet surveys and preference studies have not been conducted. In addition, species identification is rare because most wildlife researchers are not acquainted with common mushroom species and professional taxonomic help is difficult to obtain (Cowan 1945). In most field studies, mushrooms are categorized into groups such as "field mushrooms," "mixed-mushrooms," or simply "fungi." However, when listed, species of the following genera are consistently taken by deer: *Amanita* (Hungerford 1970), *Armillaria* (Healy 1971, Miller and Halls 1969), *Boletus* (Cowan 1945, Hungerford 1970, Beale and Darby 1991), *Clavaria* (Dixon 1934), *Clitocybe* (Cowan 1945, Beale and Darby 1991), *Cortinarius* (Hungerford 1970), *Morchella* (Cowan 1945), *Lactarius* (Miller and Halls 1969), *Lentinus* (Dixon 1934), *Polyporus* (Skinner and Telfer 1974), *Russula* (Cowan 1945, Miller and Halls 1969, Hungerford 1970), and *Suillus* (Miller and Halls 1969).

Mushroom Consumption by Elk

Elk (*Cervus elaphus*) diet studies rarely record fungi as a component. An extensive literature review of elk food habits in 1973 did not mention mushrooms as a recorded food item (Kufeld 1973). However, at least four studies have recorded mushrooms as a component of elk diets (Table 1). Composition estimates range from a trace to as high as 75% on a dry-weight basis (Collins et al. 1978). As with deer, mushroom consumption is greatest during seasons of greatest availability—late summer and fall.

It seems reasonable to assume that mushroom species sought by deer would also be acceptable to elk, though evidence is lacking. Collins (1977) listed species of *Aleuria*, *Boletus*, and *Russula* as important and "highly preferred" dietary components.

Mushroom Consumption by Caribou

Mushrooms have often been recorded as very palatable and highly sought dietary items in caribou (*Rangifer tarandus*) diets. When mushrooms are available, they may constitute 10–25% of caribou diets, but they may average as much as 45% (Table 1) and have been recorded as high as 84% in one individual (Skoog 1968). Even in winter, reindeer "unerringly" detect snow-covered frozen mushrooms, "consuming them greedily" (Karaev 1968). Boertje (1981) reported that most genera of mushrooms are taken without hesitation by caribou. Mushrooms of the genera *Boletus*, *Coprinus*, *Lactarius*, *Lycoperdon*, *Morchella*, and *Russula* have been listed as major dietary components (Karaev 1968, Skoog 1968, Boertje 1981).

NUTRITIVE VALUE OF MUSHROOMS

Many authors state that deer, elk, and caribou "strongly prefer" mushrooms and in some cases actually travel from site to site seeking mushrooms. The obvious question is, why? What nutritional benefits do cervids gain from fungi? Some authors consider mushrooms nearly devoid of nutrition, while others suggest they compare favorably with soybeans or spinach (Crisan and Sands 1978).

Little is known about the true nutritive value of mushrooms since few comprehensive studies have been conducted. Crisan and Sands (1978) conducted a thorough literature review on the nutritive value of wild mushrooms to monogastrics (e.g., humans). Several range and wildlife scientists have collected and analyzed mushrooms prominent in ruminant diets. But, the nutritional procedures used by most range and wildlife scientists were designed to analyze grasses and forbs. When these procedures are applied to mushrooms, the results are often incorrectly interpreted because mushrooms are much different from vascular plants in their chemical composition. Further information on the nutritive value of mushrooms can be gained from research on mycophagy by insects and small mammals. The following discussion is a summary and interpretation of nutrition studies to assess the value of mushrooms to ruminant animals.

Moisture Content of Mushrooms

Over 80% of the fresh weight of most mushrooms is water (Table 2). This large water proportion requires that the consumer eat large volumes to obtain nutritional benefit, although high water content rarely restricts intake. The

Table 2. Nutritive value and digestibility of wild mushrooms[a].

Composite samples based on:	Initial moisture	Crude protein	Ash	Fat	N-free extract	Fiber	Calcium	Phos-phorus	Digesti-bility	Source[b]
Species available	–	34.8	8.1	4.8	31.6	20.8 (crude)	–	–	–	7
Species available	–	23.0	9.0	5.0	48.0	15.0 (crude)	–	–	–	5
Species available	83.9	21.5	6.6	3.9	54.2	13.8 (crude)	0.09	0.56	–	4
Species in cattle diets (summer)	–	22.0	–	–	–	– –	<0.10	0.42	–	2
Species in cattle diets (fall)	–	25.0	–	–	–	– –	<0.10	0.55	–	2
Species available (winter)	89.4	22.1	–	–	–	– –	0.08	0.46	58.8	1
Species available (spring)	87.6	23.1	–	–	–	– –	0.07	0.47	64.7	1
Species available (summer)	87.2	29.0	–		–	– –	0.05	0.53	56.6	1
Species available (fall)	85.9	24.8	–		–	– –	0.04	0.53	59.9	1
Species in deer diets	88.9	21.3	–	–	–	– –	–	–	80.8	6
Species in elk diets	89.5	24.1	–		–	– –	–	–	77.5	6
Species in caribou diets (summer)	–	34.7	–		–	31.7 (NDF)	0.03	0.70	90.0	3
Species in caribou diets (fall)	–	35.3	–	–	–	31.5 (NDF)	0.03	0.71	90.0	3
Species in caribou diets (winter)	–	40.0	–	–	–	29.9 (NDF)	0.03	0.79	91.0	3

[a] All data expressed as a % of dry matter except initial moisture, which is expressed as % of fresh weight.

[b] Key to references: (1) Blair et al. 1984, (2) Bjugstad and Dalrymple 1968, (3) Boertje 1981, (4) Crisan and Sands 1978, (5) Kelsall 1968, (6) Pallesen 1979, (7) Svrjala-Qvist 1986.

addition of water to the rumen per se has little effect on intake because it is easily absorbed or removed (Van Soest 1982). Mushrooms may in fact be an important source of water for some mammals (Fogel and Trappe 1978).

Mushrooms as an Energy Source

Mushrooms, like true plants, contain lipids (or fats), nonstructural carbohydrates, and fiber that are all used as energy sources by ruminants. The average gross energy of mushrooms ranges from 300 to 400 kcals per 100 grams dry weight. Fleshy fungal tissue compares favorably with many fruits and vegetables but is less rich in energy than seeds or nuts (Martin 1979).

The fat content of edible mushrooms ranges from <1% to as high as 20% (Crisan and Sands 1978). On average, however, mushrooms contain 2–6% fat. The fat component of fungal tissue includes free fatty acids, mono-, di-, and triglycerides, sterols, sterol esters, and phospholipids.

On a dry-weight basis, mushrooms are primarily composed of nonstructural carbohydrates (nitrogen-free extract [Table 2]). A large variety of compounds make up the carbohydrate components, including pentoses, methyl pentoses, hexoses, disaccharides, amino sugars, sugar alcohols, and sugar acids (Crisan and Sands 1978). By comparison, the most prominent nonstructural carbohydrates in green plants are fructosans, sugars, dextrin, and starch (Trlica 1977).

In plants most energy available to ruminants comes from the microbial degradation of fibrous cell walls. However, fungal cell walls are much different from those of higher plants. The primary component of fungal cell walls is chitin, whereas plant cell walls are mostly cellulose (Crisan and Sands 1978, Martin 1979). Chitin is a N-acetylglucosamine polymer linked with β-1,4 bonds similar to cellulose. Unlike the fiber of higher plants, chitin contains a significant proportion of nonprotein nitrogen as an amino sugar. A β-glucan, with β-1,3 linkages and β-1,6 branches, also forms a part of the cell wall (Martin 1979). Additionally, lignin and pectin are not known to occur in fungi.

Protein Content of Mushrooms

Early investigators used the term "vegetable meat" to describe mushrooms because analysis revealed that native mushrooms contain 20–50% of their dry matter as protein (Peck 1895). More recent studies on mushroom protein content suggest that mushrooms probably rarely reach 50% protein by dry weight. However, relatively speaking, mushrooms are an excellent protein source. There is extreme variation in protein content from a low of about 4% to as high as 44% depending on species, stage of growth, and environmental conditions (Crisan and Sands 1978). By comparison, fresh-cut alfalfa (*Medicago sativa*) is generally 16–19% protein (Jurgens 1978).

Crude protein is usually calculated by multiplying total nitrogen, determined by Kjeldahl analysis, by 6.25. This correction factor is based on the assumptions that most proteins contain 16% nitrogen, that these proteins are completely digestible, and that amounts of nonprotein nitrogen in the cell are negligible. Since a substantial amount of nitrogen in mushrooms is in chitin and other nonprotein compounds, such as urea and nucleic acids, Crisan and Sands (1978) suggested a correction term based on the assumption that only 70% of the nitrogen in mushrooms is in the form of digestible protein (70%N * 6.25 = 4.38). This correction term of 4.38% may be conservative when considering the use of mushrooms by ruminants and comparing mushrooms to other forage eaten by ruminants. Only 60–70% of the nitrogen in fungal tissue is in the form of protein (Moore-Landecker 1982). However, this estimate is similar to the proportion of nitrogen in proteins in forage plants (60–80%; Van Soest 1982). Furthermore, nonprotein nitrogen, such as urea, is readily converted to ammonia by rumen microbes and is either used for microbial growth or absorbed across the rumen wall. The nitrogen fraction of chitin is unavailable to monogastrics but is probably converted to microbial protein in the rumen. In fact, chitinous nitrogen may be more available to ruminants than the cell-wall nitrogen of higher plants due to the lack of lignin in fungi.

Vitamin and Mineral Composition of Mushrooms

Mushrooms are a good source of several vitamins including the B complex and vitamin C (Change 1980, Crisan and Sands 1978). However, these are not essential vitamins for ruminants because they can be synthesized by rumen microbes (Van Soest 1982). Additionally, mushrooms are basically devoid of vitamins A and D, which are essential dietary components for ruminants.

Mushrooms accumulate minerals from the soil and plant material on which they grow. Therefore, mushrooms probably contain all the minerals present in their growth substrate (Crisan and Sands 1978). Stating average mineral concentrations may be misleading because mineral concentration varies greatly depending on species and soil fertility. For example, though potassium level averages 2% (in 24 species from several locations), it varies from 0.18 to 4.8% (Crisan and Sands 1978).

The most abundant minerals in mushrooms are potassium, averaging about 2% dry weight, and phosphorus, averaging about 0.75% (Change 1980, Crisan and Sands 1978, Martin 1979). Both mineral levels exceed maintenance requirements of most weaned ungulates (based on sheep and cattle requirements; Jurgens 1978). Mushrooms also contain calcium but at lower concentration than phosphorus or potassium. However, calcium concentration averages 0.14%, which would not meet calcium requirements of weaned deer (Ullrey et al. 1973). Calcium is often in excess of ruminant needs in other forages, while phosphorus is more commonly inadequate.

Digestibility of Mushrooms

The degradation of fungal cell walls requires chitinase and β-1,3 and β-1,6 glucanases (Martin 1979). Chitin is degradable in the rumen because of chitinase activity by rumen microbes, although there may be an adaptation period necessary to obtain adequate levels of chitinase activity (Cheeke 1991). The ability of rumen microbes to degrade the β-glucans in fungal cell walls is unknown.

The in vitro digestibility of mushrooms is very high relative to other ungulate forages (Table 2) and may exceed 90% in some cases. Consequently, identification of mushrooms in fecal analysis is rare (Boertje 1981).

IMPLICATIONS OF MYCOPHAGY BY DEER AND ELK

To conclude this discussion it is fair to ask, What difference does it make if deer, elk, or caribou eat mushrooms or not? Mycophagy by cervids may be important for several reasons. First, mushrooms undoubtedly make an important, though sporadic, contribution to cervid nutrition in mushroom-rich environments. Mushrooms are highly preferred and nutritious foods for cervids, particularly in late summer and fall in forested areas of western North America and throughout the year in the Southeast. Mushrooms may be a particularly important protein and phosphorus source in late season when many forages yield only enough digestible dry matter to meet basal energy requirements (Short 1975, Blair et al. 1984). Therefore, even a few bites of mushrooms by an herbivore may contribute substantially to meeting the nutritional requirements and helping to balance nutrients obtained from other forages of quite different composition.

Second, mushrooms may attract herbivores to mature and stagnated forest areas that might otherwise go unused as foraging areas (Rasmussen 1941, Collins et al. 1978, Warren and Mysterud 1991). Additionally, mushrooms may become an important dietary supplement when herbivores are forced to seek densely forested areas for protection from biting insects or predators (Bergerud 1972). Mushroom production is usually greatest in dense forested areas, in part because mushrooms do not require sunlight for growth.

Finally, fungi play an important symbiotic role in mycorrhizal relationships with several conifer species, including ponderosa pine (Kotter 1984). Since the spores of fungi are apparently not destroyed in the rumen, herbivores may serve as vectors for fungal spores to initiate mycorrhizal associations (Fogel and Trappe 1978).

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TERRESTRIAL VERTEBRATES OF THE MONO LAKE ISLANDS, CALIFORNIA

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ABSTRACT.—We compared vertebrate populations between the two major islands (Paoha and Negit) in Mono Lake, California, and the adjacent mainland to further elucidate the mechanisms underlying island colonization. Deer mice (*Peromyscus maniculatus*) and montane voles (*Microtus montanus*) were captured on Paoha, but only deer mice were captured on Negit. In contrast, eight species of rodents were captured on the mainland. Overall rodent abundance on Paoha and the mainland was similar, but on Negit it was about three times greater than on Paoha or the mainland. Adult deer mice from Paoha were significantly ($P < .05$) smaller in most external body characteristics than mainland mice. Coyotes (*Canis latrans*) and one or two species of lagomorphs were observed on the islands and the mainland. No amphibians or reptiles were found on the islands; both occurred in low numbers on the mainland. Rafting and human transport are probable means of colonization for mice and voles. The occurrence of coyotes on the islands may have modified historic predator-prey relationships, and thus the population of rodents and lagomorphs.

Key words: Mono Lake, islands, colonization, Peromyscus maniculatus, Microtus montanus, *land bridge.*

Island animal populations have attracted much scientific interest because they serve as natural experiments for the study of colonization, dispersal, extinction, competition, and other biological processes (MacArthur and Wilson 1967). Because islands are small and isolated, populations inhabiting them are more vulnerable to stochastic events than their mainland counterparts.

Most previous studies of island zoogeography have emphasized patterns of island occupancy, morphology, and genetics of restricted subsets of the islands' fauna (reviewed by Peltonen and Hanski 1991). Our goals were to compare island and mainland vertebrates of Mono Lake and the surrounding Mono Basin, California, in light of natural and human-influenced processes. This area was of interest because no thorough surveys had been conducted on the islands of this large saline lake, and because of possible changes in local ecology associated with falling lake levels from water diversion for human consumption.

MONO BASIN AND ISLANDS

Mono Basin is the hydrologic drainage basin for Mono Lake. The basin is surrounded by the Sierra Nevada to the west and the Great Basin ranges to the north, east, and south. Mono Lake, estimated at 500,000 years of age, is one of the oldest lakes in North America. Because no water naturally flows out of the basin, and because of long-term evaporation coupled with water diversion, the lake's salinity is about 2.5 times that of the ocean. In October 1986 the surface area of the lake was about 177 km^2 (Mono Basin Ecosystem Study Committee 1987).

There are two major islands in the lake: Paoha Island at about 7.7 km^2 and Negit Island at only about 1.3 km^2 (Fig. 1). Paoha formed from volcanic activity and an uplift of lake sediment some time between 1723 and 1850 A.D. Negit formed as a result of a series of eruptions beginning about 200 A.D. (Mono Basin Ecosystem Study Committee 1987, U.S. Forest Service 1989).

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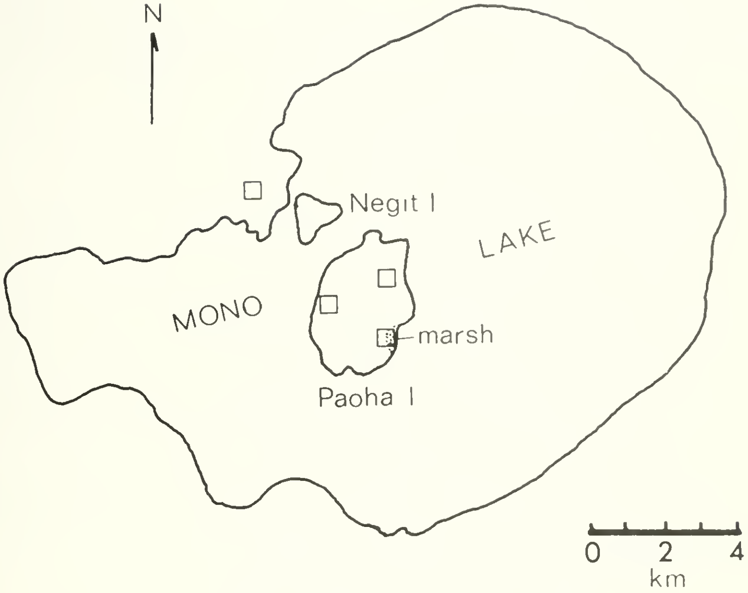

Fig. 1. Mono Lake and the two major islands, Paoha and Negit; small islets are not shown. The boxes indicate the general location of the 1991 study plots; stippling indicates the marsh on Paoha. Redrawn from various U.S. Forest Service maps.

Beginning in 1941 the major streams entering Mono Lake were diverted and their water was transported to Los Angeles, California. This diversion lowered the lake level about 15 m by 1981, to the modern historic low, and also decreased the lake volume by about 50% (Mono Basin Ecosystem Study Committee 1987, Botkin et al. 1988). Although diversions have been halted, a continuing drought (through at least 1992) that began in 1986 has prevented any significant rise in the lake level.

Paoha and Negit islands are located along an axis running perpendicular from the northern shore of Mono Lake, with Paoha the farthest away and about 1 km from Negit. Since its formation, Negit has been separated from the mainland by 0 to >3 km (Mono Basin Ecosystem Study Committee 1987: Figs. 1.3 and 6.1). However, no mainland connection with Negit existed since the formation of Paoha until the late 1970s; the next most recent land bridge apparently occurred about 500 years before present. During our study in 1990–91, Negit was separated from the mainland by several hundred meters of mudflats and a few meters of shallow water; this area is referred to herein as the land bridge.

We know of only two previous small mammal trapping efforts on the islands. In 1975 W. M. Hoffmann (unpublished report) captured no small mammals on Paoha in one night of effort. J. H. Harris (personal communication) captured deer mice (*Peromyscus maniculatus*) on Negit during several days of trapping in the early 1980s. One of us (JRJ) has made repeated visits annually to the islands since 1980, making visual observations, but not trapping. All other accounts of the islands' mammal fauna are from recollections of early settlers and local residents (e.g., Fletcher 1987, personal communication with JRJ).

STUDY AREAS

Paoha Island can be divided into two general vegetative zones: a small (about 2 ha) spring-fed marsh along the southeastern shore, and the remaining nonmarsh vegetation. Vegetation in the marsh is composed of rush (*Juncus effusus*), bullrush (*Scirpus americanus*), saltgrass (*Distichlis spicata*), foxtail (*Hordeum jubatum*), and bassia (*Bassia hyssopifolia*). Nonmarsh areas are dominated by greasewood (*Sarcobatus vermiculatus*) and hopsage (*Grayia spinosa*); sagebrush (*Artemisia tridentata*) is present but rare. Grasses and herbaceous plants are scarce and concentrated in the marsh and one small (about 0.3 ha) grassland site located upslope about 300 m from the marsh. The grassland area is dominated by exotic cheatgrass (*Bromus tectorum*). Negit Island lacks any marsh vegetation and has no permanent freshwater. The upland is similar to Paoha except for more cover by sagebrush. Dominant vegetation on the mainland plots is sagebrush, rabbitbrush (*Chrysothamnus nauseosus*), bitterbrush (*Purshia tridentata*), and scattered individuals of greasewood, curlleaf mahogany (*Cercocarpus ledifolius*), and desert peach (*Prunus andersonii*). Vegetation in the basin was detailed by Burch et al. (1977). Soils are a loose mixture of sand, gravel, ash, and silt (Loeffler 1977).

In 1990 trap lines were established to determine species composition and approximate distributions of small mammals on Paoha and Negit. Specific trap locations were based on ease of boat landing and proximity to the next nearest trapping location; adjacent trap lines were at least 200 m apart.

In 1991 we systematically established 10 fixed study plots (50 × 20 m) on Paoha Island and 5 on the adjacent mainland to compare mammals on the island and mainland; island plots were placed in the marsh (3 plots) and dry shrub vegetation (7 plots). All mainland plots were located to the north and northeast of Black Point on the northwest shore of Mono Lake. This location was selected because its vegetation resembles the dominant vegetation on Paoha Island and represents a likely source for terrestrial animals.

METHODS

Small Mammal Live-Trapping

All traps used during this study were large (7.6 × 8.9 × 22.9 cm [3 × 3.5 × 9 inch]) Sherman live-traps. In 1990 trapping was done on Paoha Island on 27–29 April and 23–25 August, Negit Island on 27–29 April, and the mainland on 4–7 September. Trap spacings ranged from 10 to 20 m and were based on availability of vegetative cover. Traps were baited with rolled oats and peanut butter and checked each morning for 1–3 days depending upon weather conditions and thus access to the islands. Mainland trapping in 1990 was restricted to a marsh on the northern shore of the lake. Captures were identified to species, sex, and age and were measured, marked, and released at the trap location. Measurements between sexes and between island and mainland populations of deer mice were compared using *t* tests (Zar 1984:126–131).

In 1991, within each plot on Paoha described above, 18 large Sherman live-traps were placed at 10-m spacings (1 row of 6 traps along each long axis of a plot). Each plot was trapped for a total of 54 trap-nights and days (i.e., traps were left open constantly for 3 days and checked both during the morning and in late afternoon). Traps were baited and animals handled as in 1990. Mainland and Paoha traps were run 7 May–24 June. Trap lines were run on Negit 4–5 August, as described for 1990. Data are reported here as the number of new individuals (i.e., excluding recaptures) captured per 100 trap-nights; we assume that this measure of capture success is an adequate index of actual population abundance. Indices of abundance were compared using chi-square goodness of fit (Zar 1984:40–43).

Other Surveys

During 1991, one 4.2-L (1-gal) can was placed near the center of each trapping plot. Cans were placed on all mainland plots and on six Paoha Island plots. Each was covered with a wooden board raised 2–3 cm above the can. Traps were run 4–17 days. Three additional traps were placed in the marsh on the southeast side of Paoha Island, this being the most likely location for shrews (Soricidae). Thus, six traps were placed in the marsh. All mainland pitfalls were opened 9–12 June; island traps were opened 7 May–4 June.

A 1-m^2 area in an open location near the center of each plot was selected to determine the presence of medium- to larger-sized mammals traveling across the plot. The soil in a track plot was smoothed by hand and moistened with water; fine-grained sand or soil was added as needed. A can of chicken-flavored cat food was secured at the center of each track plot. Each plot was checked daily for three days for evidence of wildlife use. One-half of the study plots on Paoha and three mainland study plots were used.

Time-constraint surveys of one-person-hour duration each were conducted in all study plots. The species, date, time, location, and general vegetation type for each observation were recorded.

Museum Records

We obtained records for all vertebrates collected in Mono Basin from the Los Angeles

TABLE 1. Index of abundance (no./100 trap-nights) for small mammals captured on study plots on Paoha Island (n = 10 plots) and adjacent mainland (n = 5 plots), and on Negit Island (trap lines), Mono Basin, California, 1991.[a]

	Paoha Island (trap-nights)				
Species	Total marsh (108)	Total nonmarsh (324)	Total island (432)	Negit Island (120)	Total mainland (342)
Peromyscus maniculatus	17.6	13.0	14.1	62.5	6.4
Male	8.3	9.0	8.8	32.5	4.1
Female	9.3	4.0	5.3	30.0	2.3
Microtus montanus	5.6	0.9	2.1		0.3
Perognathus parvus					6.7
Dipodomys panamintinus					5.3
D. microps					1.8
Peromyscus boylii					0.3
Eutamius minimus					0.3
Spermophilus beecheyi					0.3
Total	23.2	13.9	16.2	62.5	21.3

[a] Chi-square analysis: all comparisons between total marsh and total nonmarsh on Paoha $P > .05$; between Paoha total island and Negit Island $P < .001$, between total Paoha and total mainland $P > .05$; and between total mainland and Negit $P < .01$

County Museum of Natural History (LACMNH) and the Museum of Vertebrate Zoology, University of California, Berkeley (MVZ). Although no records were available for the islands, data from the basin were summarized to supplement published accounts of mainland vertebrate surveys. Voucher specimens were deposited at the MVZ.

RESULTS

Small Mammal Trapping

Only deer mice and montane voles (*Microtus montanus*) were captured on Paoha Island. Most voles were captured in the marsh; deer mice were also slightly more abundant there than in dry shrub plots, but these differences were not significant ($P > .1$). The sex ratio of deer mice was skewed toward males in the dry shrub, but was about even in the marsh (Table 1).

Only deer mice were captured on Negit Island. Mouse abundance was about 4.5 times higher on Negit than on Paoha ($P < .05$), and sex ratios were about even (Table 1).

Eight species of small mammals were captured on the mainland plots in 1991. Great Basin pocket mice (*Perognathus parvus*), deer mice, and Panamint kangaroo rats (*Dipodomys panamintinus*) had similar relative abundances and were the only species with abundances >5 individuals/100 trap-nights). Except for the Great Basin kangaroo rat (*Dipodomys microps*), all species were captured rarely (all at 0.3 animals/100 trap-nights). Overall abundance of small mammals on Paoha was similar to that on the mainland, but on Negit it was almost three times greater than that on Paoha ($P < .001$) or the mainland ($P < .01$; Table 1).

Abundance of deer mice approximately doubled ($P < .01$) on Paoha between April (early breeding) and August (end of breeding) 1990. Subadult males accounted for 67% of this increase (Table 2), while subadult females accounted for only 6%. Total male and female abundance was about equal in April; the number of males caught increased by 63% and females only by 35% in August, although the difference was not significant ($P > .1$).

Male and female abundances of deer mice were similar on Negit in April 1990; no comparable August data were available. Total abundance on Negit in April was 48% higher ($P < .05$) than that on Paoha (Table 2).

Adult male deer mice from Paoha weighed significantly less and had significantly shorter tails, feet, and tail:body-length ratios than mainland animals; body and ear lengths were not different (Table 3). Adult females from Paoha were significantly less heavy than mainland animals and had smaller but not significantly different average measurements for other characters. Comparisons with Negit mice were not possible because an insufficient number of animals were measured.

Other Surveys

ISLANDS.—The six pitfalls in the Paoha marsh were run for 13 days (78 trap-days) and captured 7.7 voles/100 pitfall-days; the three

TABLE 2. Abundance (no./100 trap-nights) of *Peromyscus maniculatus* on Paoha and Negit islands, Mono Lake, California, 1990.

	Paoha Island		Negit Island
	April	August	April
Trap-nights	290	160	74
Male			
Adult	7.6	8.8	13.5
Subadult	1.0	15.0^{***}	0.0
Juvenile	0.7	1.3	0.0
Total	9.3	25.0^{**}	13.5
Female			
Adult	5.9	8.1	10.8
Subadult	3.8	5.0	4.1
Juvenile	0.0	1.9	0.0
Total	9.7	15.0	14.9
Overall	19.0	40.0^{**}	36.5^{**}

Chi-square analysis $^{**}P < .01$, $^{***}P < .001$, Paoha April vs. August and Paoha April vs. Negit April.

pitfalls in the dry shrub were run for 17 days (51 pitfall-days); no animals were captured. Track plots were run for 3 days on Paoha, resulting in a total effort of 15 track-plot-days. One set of coyote (*Canis latrans*) tracks was found on a plot in the marsh, and one set of unidentified rodent tracks (likely deer mouse) was found on a dry shrub plot. Coyote tracks and scat were seen throughout both islands; they were especially evident on the southeast end of Paoha, including the marsh. Black-tailed jackrabbits (*Lepus californicus*) were uncommon but were seen occasionally on both islands. Cottontails (*Sylvilagus* spp.) were seen rarely on Negit but were not evident on Paoha. Rabbit pellets were conspicuous on the islands, indicating that the populations had been greater at a previous time. No herps were observed on either island during any survey, or in any yearly island visit by JRJ since 1980. Scattered individuals of sagebrush lizard (*Sceloporus gracious*) were seen while walking on and near the mainland study plots.

MAINLAND.—The five pitfalls were run for 4 days (20 pitfall-days). Four sagebrush lizards were captured (20 lizards/100 pitfall-days). Track plots were run for a total of 3 days on three study plots, with one set of black-tailed jackrabbit, two sets of kangaroo rat (species unknown), and one set of unidentified small rodent tracks observed. Thus, there were four separate animals in 9 track-plot-days. Coyote tracks were seen on the plots and coyotes were heard calling adjacent to plots. Numerous rabbit and kangaroo rat tracks were present on all plots; cottontails were also seen adjacent to the plots on several occasions.

DISCUSSION

Only two species of small mammal (deer mouse and montane vole) were trapped on Paoha, and one species (deer mouse) on Negit, compared with eight species—including deer mice and montane voles—on the adjacent mainland. Visual and track surveys found the jackrabbit, cottontail, and coyote on Negit Island and the mainland; all but the cottontail were evident on Paoha. In contrast, at least 20 species of small mammals have been observed around the shores of Mono Lake (Harris 1982, 1984). In addition, weasels (*Mustela* spp.), badger (*Taxidea taxus*), bobcat (*Lynx rufus*), mountain lion (*Felis concolor*), black bear (*Ursus americanus*), and mule deer (*Odocoileus hemionus*) occur around Mono Lake (Harris 1982). Furthermore, lion remains have been reported from an islet near Negit and from the vicinity of the Negit-mainland land bridge (Mono Lake Committee, unpublished observation). The presence of montane voles on Paoha was associated with the marsh and grass vegetation that is absent on Negit. The current lake level has allowed the Paoha marsh to expand onto an exposed lake shelf, thus increasing potential vole habitat. The environment may be unsuitable on the islands for persistence of the larger carnivores and deer but appears suitable on Paoha (because of water and rodents) for weasels and possibly badgers.

Animals can colonize islands by swimming, rafting, using ice bridges, being inadvertent passengers on watercraft (Calhoun and Greenbaum 1991), intentional or unintentional releases, or by flying; all but flying may apply to the animals discussed herein. The lack of historic, quantitative data, however, prevents determination of the method(s) and date(s) of arrival of animals on the Mono Lake islands. However, Hoffman (unpublished report) set 76 Sherman traps for one night (24 May) in 1974 in various locations, including in and around the same marsh and grassland areas we trapped. He caught no animals but did locate a rodent faex. Although Hoffman's efforts were minimal, his data at least indicate the presence of rodents prior to 1974.

Although the earliest historic accounts of local Native Americans date to the early 1860s (Jehl et al. 1984, 1988), various peoples are

TABLE 3. Characteristics of adult *Peromyscus maniculatus* captured on Paoha Island, Mono Lake, and adjacent mainland during 1990 and 1991.

	Adult male[a]				Adult female[b]			
	Paoha		Mainland		Paoha		Mainland	
Characteristic	$\bar{X}$	SD	$\bar{X}$	SD	$\bar{X}$	SD	$\bar{X}$	SD
Mass (g)[c]	17.2	2.11	18.8	1.29**	18.1	2.29	19.9	2.80
Body length (mm)	81.4	5.13	81.4	2.87	79.4	6.50	81.1	3.18
Tail length (mm)	64.5	4.32	67.1	5.34*	66.4	6.85	69.1	6.34
Foot (mm)	20.0	1.07	20.9	0.95**	20.0	0.91	20.6	1.08
Ear (mm)	17.4	1.08	17.4	1.45	17.4	1.04	17.9	1.38
Tail/body	0.79	0.06	0.82	0.07*	0.84	0.07	0.85	0.07

[a] Sample size = 50 individuals each area, except for mass.
[b] Sample size = 15 individuals each area, except for mass.
[c] Excludes pregnant females. Paoha $n = 12$, mainland $n = 13$.
*$P < .05$ **$P < .01$ t test.

thought to have visited the basin for a much longer period (Fletcher 1987). Western immigrants began making trips to the islands by the 1860s (Jehl et al. 1984, 1988, Fletcher 1987). A chicken (*Gallus gallus*) and domestic lagomorph ranch was established on Paoha in the late 1870s, a domestic goat (*Capra* sp.) ranch was initiated in the 1890s (Fletcher 1987), and a mineral salts and health spa venture was attempted in the 1940s. Lagomorphs raised commercially were apparently European hares (*Lepus* sp.), but there is no evidence that these hares remained on Paoha after the early 1920s when the commercial operation ceased. A few goats survived on Paoha until at least 1975 (Hoffman, unpublished report) but were extirpated by 1980.

Thus, human movements onto the islands were frequent, and rodents, such as deer mice and voles, could have been inadvertently transported in the grain, hay, and other items taken to support activities on the islands. We do not know if native lagomorphs were tranported to the islands by humans.

There is debate in the literature over the abilities of *Peromyscus*, *Microtus*, and other small mammals to colonize islands by swimming or rafting because they are not well adapted for exposure to water (Redfield 1976, Calhoun and Greenbaum 1991, Peltonen and Hanski 1991). We have no direct way of quantifying the relative probabilities of inadvertent human transport versus rafting. However, the known and frequent history of human visitation and habitation for commercial purposes during this century results in a higher frequency of occurrence and less harsh means of possible transport than does rafting due to flooding events. Confounding the present situation is the land bridge or near land bridge. Movement across the land bridge to Negit, followed by swimming or rafting to Paoha, is likely more probable now than historically.

The absence of lizards on the islands is perplexing, however, as there appears to be ample habitat on the islands, and species on the mainland are potentially good colonizers (*sensu* Case 1975, 1983). However, mainland populations are small, as the elevation of the Mono Basin is at the upper end of the normal range for reptiles in the Sierra Nevada (summarized from Storer and Usinger 1968). Therefore, their chance of arrival and persistence is low.

Snakes (*Pituophis melanoleucus* and *Thamnophis elegans*) and amphibians (*Bufo boreas*, *Hyla regilla*, *Scaphiopus hammondii*, *S. intermontanus*) are found around Mono Lake (MVZ specimens, personal observation), but they are scarce locally (personal observation). There are no historic records of snakes or amphibians on either island, and we saw no evidence of either during our visits. As discussed above for lizards, it appears that the chance of arrival and persistence of snakes and amphibians is low.

The Mono Lake islands parallel other islands in having a greater population abundance (especially Negit) and a simple species composition relative to the mainland. Larger relative abundances may be because few predators are present and the lack of nonavian food competitors, as has been postulated for other island rodent populations (e.g., Halpin and Sullivan 1978). The few rodent species, absence of lizards, and reduced bird-species richness (Hall et al., in preparation) on the islands may result in density compensation (*sensu* MacArthur et al. 1972, Case 1975) by the islands' *Peromyscus* populations.

In contrast to island biogeographic theory (Redfield 1976, Sullivan 1977), deer mice are smaller on the islands than on the mainland. Although a founder effect (*sensu* Kilpatrick 1981, Calhoun and Greenbaum 1991) could have resulted in smaller individuals on the islands than on the mainland, there is likely some combination of ecological factors on the Mono Lake islands that has either resulted in maintenance of small body size or has directed selection toward smaller body size. In our study the sex ratio of deer mice appears to be male biased, although more intensive trapping, both within and between years, would be necessary for confirmation because of potential trapping biases associated with dispersing young males.

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VASCULAR FLORA OF KANE LAKE CIRQUE, PIONEER MOUNTAINS, IDAHO

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ABSTRACT.—Kane Lake Cirque lies in the western Pioneer Mountains of south central Idaho. An inventory of the high-elevation flora of the cirque revealed the presence of 180 vascular taxa representing 95 genera and 30 families. Five alpine taxa are here documented from Idaho for the first time: *Carex incurviformis* Mack., *Draba fladnizensis* Wilfen., *Potentilla nivea* L., *Ranunculus gelidus* Kar. & Kir., and *Ranunculus pygmaeus* Wahlenb. Kane Lake Cirque also contains populations of four additional alpine taxa considered to be of conservation concern in Idaho: *Erigeron humilis* Graham, *Parnassia kotzebuei* Cham., *Saxifraga adscendens* L., and *Saxifraga cernua* L.

Key words: Idaho, Pioneer Mountains, Kane Lake Cirque, alpine vascular flora, state records, rare flora.

Studies of alpine flora have been numerous throughout the North American Cordillera, but only recently have investigations of this kind been undertaken in Idaho. Floristic studies initiated by Douglass Henderson of the University of Idaho Herbarium in the mid-1970s were the first to systematically explore the alpine zone of Idaho. Through numerous collections, he and co-workers documented Idaho's alpine flora to be unique in many respects (Henderson 1978, Brunsfeld 1981, Henderson et al. 1981, Brunsfeld et al. 1983, Caicco et al. 1983, Lackshewitz et al. 1983, Hartman and Constance 1985). Nearly all these investigations took place in the large Basin and Range-like massifs in east central Idaho, with few extending into the western Pioneer Mountains of south central Idaho.

Rare plant inventories initiated by the U.S. Forest Service were the first to point out the phytogeographic importance of the cirques in the western Pioneer Mountains, in general, and Kane Lake Cirque, in particular (Caicco and Henderson 1981, Brunsfeld et al. 1983). Barbara Ertter's collections in 1977 and our collections in 1987 further highlighted the significance of Kane Lake Cirque. Because of increasing recreational use of the Kane Lake area, sensitivity of the habitats, and preliminary nature of the floristic inventory, we undertook this study in cooperation with the Challis National Forest to provide them with adequate data on the distribution and abundance of rare plants and habitats in the basin for future management.

STUDY AREA

The Pioneer Mountains rise abruptly from the northern edge of the Snake River Plain in central Idaho between the Big Lost and Big Wood rivers. These mountains form a large, complex block about 60 km long and 50 km wide, oriented northwest to southeast. Topography varies from sharp horns, serrate ridges, and broad upland surfaces in the alpine zone to steep-sided valleys and rounded ridges in the foothills. Elevations range from 1900 m in the valleys on the western slope to 3658 m at the summit of Hyndman Peak.

The Pioneer Mountains are composed of Tertiary Challis Volcanics consisting of interbedded lava and tuffaceous units, which lie unconformably over a core of Precambrian metamorphic and Paleozoic sedimentary units. During the formation of the Cretaceous Idaho Batholith, small "satellite" intrusive bodies were emplaced in the western Pioneer Mountains. Tertiary and Quaternary block faulting is believed to be the cause of the subsequent uplift and present relief (Dover 1981). The geomorphologic setting has been greatly influenced by Quaternary glacial and fluvial activity. Most streams in glaciated valleys are underfit, and uplands display classic alpine-type glaciated features including cols, aretes, horns, and cirques (Evenson et al. 1982).

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The Pioneer Mountains lie in a transition zone between the maritime climate of northern and western Idaho and the continental climate of southeastern Idaho, and are affected by two basic storm patterns. From November through March most precipitation comes from low-altitude cyclonic storms that move eastward from the Pacific Ocean. During May and June most precipitation results from high-altitude convectional storms moving northward from the Gulf of Mexico and California coast. The combination of maritime and continental influence creates two wet seasons, winter and late spring, respectively (Caicco 1983). No climatic data are available from high elevations in the Pioneer Mountains; however, Moseley (1985) estimates mean annual precipitation at 2835 m in the southern part of the range to be 813 mm. Throughout the mountainous regions of the world, the altitude of upper treeline has long been observed to coincide with the 10 C isotherm of the warmest month (Griggs 1937, Daubenmire 1954, Wardle 1974). Extrapolation of temperatures from valley stations in the vicinity to timberline (3000 m) using an adiabatic lapse rate of 0.62 C/100 m (Baker 1944) substantiates this observation for the Pioneer Mountains.

DESCRIPTION OF KANE LAKE CIRQUE

Kane Lake Cirque encompasses approximately 567 ha at the head of Kane Creek in the western Pioneer Mountains 21 km northeast of Ketchum, Custer County, Idaho (43°44′N 114°6′W; T5N R20E, Boise Meridian). The cirque is characterized by permanent snowfields, glacially scoured bedrock (gneiss and quartz diorite), and unstable talus and morainal deposits. Although several small ponds are scattered throughout the basin, 5.3-ha Kane Lake is the only large body of water. Elevations of the study area range from 2800 m to 3648 m. The only appreciable soil development is in depositional areas such as along streams and rivulets, around ponds and lakes, and in the coniferous woodland on the north side of Kane Lake.

Vegetation in the cirque reflects a moister regime than has been noted at high elevations elsewhere in Idaho (Brunsfeld 1981, Caicco 1983, Moseley 1985). This mesic environment can be attributed to several factors, including the north-facing orientation of the cirque, a massive headwall on the south, and high peaks on the east, south, and west sides of the basin. These features contribute collectively to a heavy snow accumulation in the winter and its retention throughout the summer. Late-lying snow and an impermeable substrate, augmented by summer thundershowers, appear to provide plentiful moisture to nearly all habitats throughout the growing season, except the south-facing slopes north of Kane Lake.

Habitats in the cirque can be divided into two distinct groups: subalpine and alpine. Subalpine vegetation is restricted to areas immediately adjacent to Kane Lake and generally does not exceed 2850 m. Alpine habitats cover most of the area and are generally sparsely vegetated, although small areas with continuous vegetative cover occur along streams and rivulets throughout the basin and contain much of the plant species diversity of the alpine zone. Plant associations of the study area are not included in published vegetation classifications of the region and are subjectively characterized below.

Subalpine Communities

Coniferous woodland. Open stands of *Pinus albicaulis* Engelm., with lesser amounts of *Abies lasiocarpa* (Hook.) Nutt. and *Picea engelmannii* Parry, occupy the level bench north of Kane Lake. The relatively xeric understory is characterized by *Vaccinium scoparium* Leiberg, *Poa nervosa* (Hook.) Vasey, and *Senecio streptanthifolius* Greene.

Upland meadows. Interspersed in low-lying areas within the coniferous woodland are meadows dominated by graminoids and forbs. Species characteristic of these sites include *Festuca idahoensis* Elmer, *Danthonia intermedia* Vasey, *Erigeron simplex* Greene, *Carex microptera* Mack., and *Potentilla diversifolia* Lehm.

Tree islands and krummolz. Isolated tree islands, consisting of small, upright *Abies lasiocarpa* with an understory dominated by *Phyllodoce* spp., occur as high as 3050 m on benches south of the lake. These relatively moist sites are surrounded by bedrock or alpine meadow communities. Areas of krummholz are rare in the study area. Small isolated patches consisting of low-growing *A. lasiocarpa* and

Pinus albicaulis occur as high as 3230 m on the steep south-facing slopes north of Kane Lake.

Lakeside meadows. Surrounding Kane Lake and radiating out along inlet and outlet streams are meadows that have soil saturated to the surface and are high in organic matter. *Carex scopulorum* Holm is dominant here along with scattered forbs, such as *Erigeron peregrinus* (Pursh) Greene, *Senecio cymbalarioides* Buek., and *Gentiana calycosa* Griseb. Low shrubs, including *Salix planifolia* Pursh and *Ledum glandulosum* Nutt., occur occasionally in these meadows.

Alpine Communities

Meadows. This mesic community is limited in extent and generally occurs in isolated patches around seeps or as stringers along streams and rivulets. *Deschampsia cespitosa* (L.) Beauv. is by far the dominant species here, with a high diversity of forbs and other graminoids occurring in low cover.

Cliffs and ledges. This is the most common community in the cirque. Most cliffs and ledges are north-facing and wet to mesic, with *Draba lonchocarpa* Rydb. being the most constant species, along with several species of *Saxifraga*. The xeric counterparts occur only on the south-facing slopes northeast of Kane Lake and have few vascular plants.

Talus and scree. Common at upper elevations in the cirque, this relatively mesic community is characterized by a unique suite of species able to withstand constantly shifting substrates. Species characteristic of material greater than 5 cm in diameter (talus) include *Hulsea algida* Gray and *Senecio fremontii* T. & G., while *Saxifraga cernua* L., *Luzula spicata* (L.) DC., and *Androsace septentrionalis* L. characterize small-diameter material (scree).

Fellfield. Dry fellfield habitats are rare, occurring only in small pockets on bedrock slabs on the cirque floor east of Kane Lake. Species typical of this poorly developed community include *Potentilla brevifolia* Nutt., *Juncus drummondii* E. Meyer, and *Sibbaldia procumbens* L. *Carex elynoides* Holm also occurs in this community but does not develop into the extensive turfs that are found elsewhere in central Idaho (Caicco 1983). All ridges surrounding the basin, typical sites for fellfield communities elsewhere in the state, are sharp aretes with no well-developed vegetation.

METHODS

The checklist is based on 263 collections, made mostly by the authors in July and August 1987 and July 1991. Other collectors include Barbara Ertter, who visited Kane Lake in July 1977, and Steven Caicco, who collected in the cirque during July 1981 and August 1982. A nearly complete set of specimens is deposited at the University of Idaho Herbarium (ID), with duplicates distributed widely. Ertter's collections are deposited at the Albertson College of Idaho (CIC).

Collections thought to be new records for Idaho were confirmed by experts in a particular taxon and/or from a search of up to 59 local, regional, and national herbaria (Moseley 1989). Range-extension data for these state-record taxa were determined from herbarium records and from the atlases and data bases maintained by the Idaho Conservation Data Center and Montana Natural Heritage Program on the location, distribution, numbers, and condition of rare plant populations in their respective states (Jenkins 1986). The Idaho Conservation Data Center data base was also consulted concerning the current distribution of additional rare species in Idaho.

RESULTS AND DISCUSSION

The vascular flora of Kane Lake Cirque consists of 180 species representing 95 genera in 30 families of pteridophytes, gymnosperms, and angiosperms. Of these, 53 species (29%) are restricted to subalpine communities in the cirque, while 58 species (33%) are restricted to alpine habitats. The remaining 69 species (38%) transcend the subalpine-alpine boundary and occur in both types of communities. Our collections of five species from the study area represent their first documented occurrence in Idaho. In addition, four other arctic-alpine species are known from Idaho from only a few occurrences and are considered rare in the state (Moseley and Groves 1990). Only one alien taxon, *Taraxacum officinale* Weber, was found in the study area.

Taxa New to Idaho

***Carex incurviformis* Mack.** This species occurs in two areas of the North American Cordillera: var. *incurviformis*, known from the Rocky Mountains of British Columbia, Alberta, Montana, and now Idaho; and var. *danaensis* (Stacey) Hermann, occurring in the southern Rocky Mountains of Colorado and the Sierra Nevada and White Mountains of California (J. Mastrogiuseppe, Washington State University, personal communication, 1991). The population in Kane Creek is disjunct south from the next closest known population in Deer Lodge County, Montana, by about 260 km (*Lackschewitz 3938* MONTU; Lesica and Shelly 1991). We found one small population in the Kane Lake Cirque, occurring in a steeply sloping meadow on seepy ledges at 3350 m at the southern end of the cirque.

***Draba fladnizensis* Wilfen.** A widespread circumpolar species, *Draba fladnizensis* is sparsely distributed in North America, from the arctic south through the Rocky Mountains to Utah and Colorado (Hitchcock 1941). As with*Carex incurviformis*, the Kane Lake Cirque population is disjunct south from the next closest known population in the Storm Lake area of the Pintlar Range, Deer Lodge County, Montana, by about 260 km (*Lackschewitz 6120* MONTU). Several very small populations occur on ledges and in rocky areas south of Kane Lake, including spray zones of waterfalls, bare stream gravels, and on steep, rocky slopes near seeps.

***Potentilla nivea* L.** This circumpolar species occurs in arctic and alpine regions of North America, being previously known in western North America from Alaska south along the main crest of the Rocky Mountains to Montana, Wyoming, Colorado, and Utah and east to Nevada (Hitchcock and Cronquist 1973). The Kane Lake Cirque population is disjunct from the nearest Montana populations by perhaps 280 km. A small population of about a dozen plants was seen in a moist, sloping meadow at the top of the waterfalls south of Kane Lake at 2950 m.

***Ranunculus gelidus* Kar. & Kir.** A North American endemic, this species is distributed across the arctic, southward in the Rocky Mountains to Colorado (Benson 1948). The very small population in Kane Creek Cirque represents a disjunction southwestward of about 350 m from the Beartooth Plateau, Stillwater County, Montana (*Stickney 4* MRC; Lesica and Shelly 1991). In the study area it occurs in a stringer of *Deschampsia cespitosa* along the northeastern tributary of Kane Lake at about 3170 m.

***Ranunculus pygmaeus* Wahlenb.** This buttercup is circumpolar, occurring south along the Rocky Mountain crest to Colorado (Benson 1948). Its presence in the Kane Lake Cirque represents a disjunction of about 200 km southwest from the next nearest known populations in the Pioneer Mountains, Beaverhead County, Montana (*Hitchcock and Muhlick 12899* WS). *Ranunculus pygmaeus* is relatively common in the Kane Lake Cirque, occurring in moist, exposed soil along creeks, on ledges and slopes, and occasionally in cracks in cliffs.

Additional Rare Species

***Erigeron humilis* Grahm.** This circumpolar species was not known from Idaho until Henderson et al. (1981) reported it from the Lemhi and Lost River ranges. Eight occurrences are now known from the state, with the Kane Lake Cirque populations being the only ones known outside the two ranges mentioned above (unpublished data on file at the Idaho Conservation Data Center, Boise). *Erigeron humilis* is relatively common in moist *Deschampsia cespitosa* meadows throughout the lower portion of the cirque.

***Parnassia kotzebuei* Cham.** This species was also not known from Idaho until recently when Brunsfeld et al. (1983) reported it from the Lost River Range and Pioneer Mountains. Four occurrences are now known from the state (unpublished data on file at the Idaho Conservation Data Center, Boise). It is relatively common on moist ledges and in sloping *Deschampsia cespitosa* meadows throughout the lower portion of the cirque.

***Saxifraga adscendens* L.** The North American representative of this wide-ranging species, var. *oregonensis* (Raf.) Breit., occurs throughout the Rocky Mountains and northern Cascade Range (Hitchcock and Cronquist 1973). In Idaho it is known from nine sites in the White Cloud Peaks, Pioneer Mountains, and Lost River Range (unpublished data on file at the Idaho Conservation Data Center, Boise). Kane Lake Cirque populations occur throughout the area on moist scree, sand, and gravel, often along streams.

***Saxifraga cernua* L.** Seven small populations of this circumboreal species are known from Idaho (unpublished data on file at the Idaho Conservation Data Center, Boise). At Kane Lake Cirque it is widely scattered in small populations from moist subalpine ledges north of Kane Lake at 2800 m to ledges and cracks on the headwall at 3400 m.

Annotated Checklist of Vascular Plants

The checklist is arranged by division and class (in Magnoliophyta), then alphabetically by family, genus, and species within these major groupings. Nomenclature generally follows Hitchcock and Cronquist (1973), exceptions being *Salix* (Brunsfeld and Johnson 1985), *Carex incurviformis* and *C. scopulorum* var. *bracteosa* (Hermann 1970), and *Eriogonum capistratum* (Reveal 1989). Unless otherwise noted, the collection numbers are the authors'.

Division Lycopodiophyta

Selaginellaceae

***Selaginella densa* Rydb.** Common in subalpine and alpine zones; moist to dry slopes and ledges and stabilized scree. 2245.

Division Polypodiophyta

Polypodiaceae

***Cryptogramma crispa* (L.) R. Br.** Uncommon in moist subalpine and alpine talus; circumboreal. 2292.

***Cystopteris fragilis* (L.) Bernh.** Common among rocks in moist alpine sites; circumboreal. 2294.

***Pellaea breweri* D.C. Eat.** Uncommon in subalpine and alpine zones; stabilized scree, rocky ledges, and boulder fields. 2293.

***Woodsia scopulina* D.C. Eat.** Common on rocks in subalpine zone. 2252.

Division Pinophyta

Cupressaceae

***Juniperus communis* L. var. *montana* Ait.** Rare on dry ledges of lower alpine zone and in krummholz. 2355.

Pinaceae

***Abies lasiocarpa* (Hook.) Nutt.** Common in woodland and krummholz communities. 2392.

***Picea engelmannii* Parry.** Common in woodland and krummholz communties. 2391.

***Pinus albicaulis* Engelm.** Common in woodland and krummholz communities. 2263.

Division Magnoliophyta

Class Magnoliopsida

Apiaceae

***Lomatium idahoense* Math. & Const.** Rare in disturbed microsites in moist subalpine meadows north of Kane Lake. 2256.

***Osmorhiza chilensis* H. & A.** Uncommon in deep soil of forest understory. 2376B.

Asteraceae

***Achillea millefolium* L. ssp. *lanulosa* (Nutt.) Piper var. *alpicola* (Rydb.) Garrett.** Common on dry subalpine and alpine slopes. 2262.

***Agoseris aurantiaca* (Hook.) Greene.** Uncommon in subalpine meadows north of Kane Lake. 2387.

***Antennaria alpina* (L.) Gaertn. var. *media* (Greene) Jeps.** Common in moist, sandy soil in alpine zone. 1186, 2336.

***Antennaria dimorpha* (Nutt.) T. & G.** Rare in dry forest opening north of Kane Lake. 2393.

***Antennaria microphylla* Rydb.** Common on dry subalpine and alpine slopes. 2244.

***Antennaria umbrinella* Rydb.** Common in dry to moist subalpine and alpine meadows. 2308, 2312.

***Arnica latifolia* Bong. var. *gracilis* (Rydb.) Cronq.** Common in deep soil of subalpine and alpine slopes and boulder fields. 2246.

***Arnica mollis* Hook.** Common in moist subalpine and lower alpine meadows and boulder fields. 1177, 2319, 2343.

***Artemisia michauxiana* Bess.** Uncommon in moist, unstable, rocky drainage bottoms; subalpine and lower alpine zones. 2363.

***Artemisia tridentata* Nutt.** Rare on dry subalpine slopes north of Kane Lake. 2261.

***Aster alpigenus* (T. & G.) Gray var. *haydenii* (Porter) Cronq.** Dry openings in forest north of Kane Lake. 2419.

***Aster foliaceus* Lindl. var. *apricus* Gray.** Common in moist alpine meadows east of Kane Lake. 1175.

***Aster stenomeres* Gray.** Dry, rocky ledges in forest openings north of Kane Lake. 2235.

***Chaenactis alpina* (Gray) Jones.** Uncommon in subalpine and alpine dry, sandy scree. 2361.

***Cirsium tweedyi* (Rydb.) Petr.** Common in moist meadows and on ledges in alpine zone. 2378.

***Erigeron acris* L. var. *debilis* Gray.** Common in moist, sandy soil; subalpine and alpine zones. 1183, 2287, 2344.

***Erigeron asperuginus* (Eat.) Gray.** Dry slopes and ledges; common in subalpine and uncommon in lower alpine zones. 2250, 2350.

***Erigeron compositus* Pursh var. *glabratus* Macoun.** Common on dry subalpine and alpine ledges. 2265.

***Erigeron coulteri* Porter.** Rare in alpine meadows along creek east of Kane Lake. 1174.

***Erigeron humilis* Graham.** Locally common in moist alpine meadows. 2274, 2410; Caicco 284.

***Erigeron peregrinus* (Pursh) Greene ssp. *callianthemus* (Greene) Cronq. var. *scaposus* (T. & G.) Cronq.** Common in moist to wet subalpine meadows around Kane Lake. 2306, 2367.

***Erigeron simplex* Greene.** Common in subalpine and alpine zones; moist meadows and slopes. 1188, 2270, 2338. Caicco 476; Ertter 2108.

***Haplopappus lyallii* Gray.** Uncommon on dry alpine ledges. 2402.

***Haplopappus macronema* Gray.** Uncommon on dry subalpine knoll, within forest north of Kane Lake. Not collected.

***Haplopappus suffruticosus* (Nutt.) Gray.** Uncommon on dry subalpine knoll, within forest north of Kane Lake. Not collected.

***Hieracium gracile* Hook.** Uncommon in dry forest openings north of Kane Lake. 2305.

***Hulsea algida* Gray.** Common in alpine talus. 2403.

***Microseris nutans* (Geyer) Shultz-Bip.** Uncommon in subalpine meadows north of Kane Lake. 2385.

***Senecio cymbalarioides* Buek.** Common in moist subalpine and alpine meadows. 1173.

***Senecio fremontii* T. & G. var. *fremontii*.** Common in alpine talus. 2400.

***Senecio streptanthifolius* Greene.** Common in subalpine zone; dry slopes and forest understory. 2255.

Solidago multiradiata Ait. var. _scopulorum_ Gray. Dry, rocky subalpine and alpine ledges. 2258.

Taraxacum lyratum (Ledeb.) DC. Common in alpine zone; moist meadows and slopes. 1185, 2289.

Taraxacum officinale Weber. Alien; rare in subalpine meadows north of Kane Lake. 2388.

Boraginaceae

Mertensia ciliata (Torr.) G. Don. Common along subalpine and lower alpine rivulets. 2268.

Brassicaceae

Arabis sp. Immature and unidentifiable to species. Uncommon in dry to moist forest openings north of Kane Lake. 2375.

Arabis lemmonii Wats. var. _lemmonii_. Common on dry, unstable alpine slopes. 2313, 2356.

Arabis microphylla Nutt. var. _microphylla_. Common on subalpine ledges and slopes north of Kane Lake. 2248.

Arabis microphylla Nutt. var. _saximontana_ Rollins. Uncommon in moist soil of alpine zone. 2374.

Draba sp. Unable to identify; possibly a new taxon. Rare; seen only in one small, steeply sloping, moist meadow at 3353 m, east of Kane lake. 2412.

Draba fladnizensis Wilfen. Circumpolar; rare on disturbed, bare-soil microsites of steep alpine slopes and along rivulets. 1107.

Draba lonchocarpa Rydb. var. _lonchocarpa_. Common throughout cirque on moist ledges and slopes; alpine zone. 1106, 2314; Ertter 2106.

Draba oligosperma Hook. var. _oligosperma_. Rare on dry alpine slopes and ledges. 2357, 2362; Ertter 2102.

Draba paysonii Macbr. var. _treleasii_ (Schulz) Hitchc. Uncommon in dry, sandy alpine soil. 2405.

Erysimum asperum (Nutt.) DC. Rare in dry subalpine talus north of Kane Lake. 2377.

Smelowskia calycina (Steph.) C.A. Mey. var. _americana_ (Regel & Herd) Drury & Rollins. Uncommon on dry, exposed alpine slopes 2349; Ertter 2107.

Caryophyllaceae

Arenaria aculeata Wats. Dry, sandy slopes; common in subalpine and rare in alpine zone. 2236, 2351.

Arenaria congesta Nutt. Uncommon on dry alpine slopes east of Kane Lake. 1187.

Arenaria obtusiloba (Rydb) Fern. Dry, exposed slopes and ledges; common in alpine and uncommon in subalpine zone. 2354.

Arenaria rubella (Wahlenb.) J.E. Smith. Circumboreal; uncommon on moist to dry alpine ledges. 2424.

Cerastium berringianum Cham. & Schlecht. Common in alpine zone throughout cirque; moist slopes, meadows, and ledges. 2321, 2413.

Sagina saginoides (L.) Britt. Circumboreal; uncommon in moist alpine meadows. 1179, 2260.

Silene douglasii Hook. var. _douglasii_. Dry, rocky ledges; uncommon in subalpine and lower alpine zone. 2364.

Silene repens Pers. var. _australe_ Hitchc. & Mag. Rare among rocks of boulder field east of Kane Lake. Caicco 286.

Stellaria longipes Goldie var. _altocaulis_ (Hulten) Hitchc. Uncommon in moist, sandy sites and scree in alpine meadows. 1180, 2327.

Stellaria umbellata Turcz. Rare in wet to moist gravels along alpine rivulets. 2326, 2347.

Crassulaceae

Sedum lanceolatum Torr. var. _lanceolatum_. Common on moist to dry subalpine and alpine slopes and ledges. 2240.

Ericaceae

Kalmia microphylla (Hook.) Heller. Common in moist to wet subalpine and alpine meadows. 2304.

Ledum glandulosum Nutt. var. _glandulosum_. Common in moist subalpine forest and meadows around Kane Lake. 2303.

Phyllodoce empetriformis (Sw.) D. Don. Common on moist subalpine and alpine slopes. 2300.

Phyllodoce glandulifera (Hook.) Cov. Common on moist subalpine and alpine slopes. 2302.

x **_Phyllodoce intermedia_ (Hook.) Camp.** Common on moist subalpine and alpine slopes. 2301.

Vaccinium scoparium Leiberg. Common in dry sites in understory of forest and krummholz. 2237.

Fabaceae

Astragalus alpinus L. Circumboreal. Common in moist meadows throughout cirque; subalpine and alpine zones. 2318, 2373; Caicco 474.

Astragalus eucosmus Robins. Rare in cracks of moist cliff near stream; alpine zone. 2396.

Astragalus kentrophyta Gray var. _implexus_ (Canby) Barneby. Common on exposed, dry alpine slopes and ledges. 2352; Ertter 2102.

Trifolium longipes Nutt. var. _pedunculatum_ (Rydb.) Hitchc. Uncommon in deep soil along subalpine streambank north of Kane Lake. 2380.

Gentianaceae

Frasera speciosa Dougl. Uncommon in dry subalpine talus north of Kane Lake. 2415.

Gentiana calycosa Griseb. var. _asepala_ (Maguire) Hitchc. Common in moist subalpine and low alpine meadows. 1172.

Gentiana prostrata Haenke. Rare; seen only in moist, steeply sloping meadow above ponds east of Kane Lake; alpine zone. 2408.

Grossulariaceae

Ribes cernuum Dougl. var. _inebrians_ (Lindl.) Hitchc. Uncommon in subalpine and alpine zones; dry ledges and boulder fields. 2409.

Ribes hendersonii Hitchc. Rare and local in dry boulder field east of Kane Lake; alpine zone. 2416.

Ribes lacustre (Pers.) Poir. Uncommon along subalpine creek near outlet of Kane Lake. 2398.

Ribes montigenum McClatchie. Common in boulder fields and dry forest understory; subalpine zone. 2310.

Hydrophyllaceae

Phacelia hastata Dougl. var. _alpina_ (Rydb.) Cronq. Uncommon in moist to dry alpine talus. 2406.

Onagraceae

Epilobium alpinum L. var. _alpinum_. Common on moist, unstable subalpine and alpine slopes; circumboreal. 2333.

Epilobium angustifolium L. Rare in dry forest opening north of Kane Lake. 2418.

Epilobium glaberrimum Barbey var. _fastigiatum_

(Nutt.) Trel. Uncommon in moist meadow along stream east of Kane Lake; alpine. 2258.

***Oenothera andina* Nutt.** Rare in disturbed microsites in dry subalpine meadows north of Kane Lake. 2264.

Polemoniaceae

***Phlox pulvinata* (Wherry) Cronq.** Common on dry, exposed alpine slopes. 2348.

***Polemonium viscosum* Nutt.** Common throughout cirque in talus and unstable sites on ledges; alpine. 2311; Ertter 2104.

Polygonaceae

***Eriogonum caespitosum* Nutt.** Uncommon on dry subalpine knoll north of Kane Lake. 2359.

***Eriogonum capistratum* Rev. var. *capistratum*.** Locally common in subalpine and alpine zones; dry, rocky slopes and ledges. 2360.

***Eriogonum ovalifolium* Nutt. var. *depressum* Blank.** Common in subalpine and alpine zones; dry, unstable slopes and ledges. 2249.

***Oxyria digyna* (L.) Hill.** Circumboreal. Common throughout cirque on moist, rocky slopes; alpine zone. 2286.

***Polygonum bistortoides* Pursh.** Common in moist to wet subalpine and alpine meadows. 2267.

***Polygonum kelloggii* Greene.** Uncommon in dry forest openings. 2390.

***Polygonum viviparum* L.** Common in moist alpine meadows. 2395; Caicco 477.

Portulacaceae

***Claytonia megarhiza* (Gray) Parry var. *megarhiza*.** Uncommon in alpine talus. 2404.

***Lewisia pygmaea* (Gray) Robins. var. *pygmaea*.** Common in dry subalpine and alpine sites. 2271, 2369.

Primulaceae

***Androsace septentrionalis* L.** Common on dry, sandy alpine slopes; circumboreal. 2353, 2422.

***Dodecatheon pulchellum* (Raf.) Merrill var. *watsonii* (Tidestrom) Hitchc.** Common in moist subalpine and alpine meadows. 2341.

Ranunculaceae

***Anemone parviflora* Michx.** Rare in moist alpine meadow south of Kane Lake. 2339.

***Aquilegia formosa* Fisch.** Common in moist, sloping meadows; subalpine and lower alpine zones. 2269; Caicco 472.

***Caltha leptosepala* DC. var. *leptosepala*.** Common throughout cirque in alpine and subalpine zones; wet meadows along streams and around lakes and ponds. 1181, 2298.

***Delphinium depauperatum* Nutt.** Uncommon in dry subalpine meadows north of Kane Lake. 2257.

***Ranunculus eschscholtzii* Schlecht. var. *eschscholtzii*.** Common throughout cirque on moist subalpine and alpine slopes. 2284; Ertter 2109.

***Ranunculus gelidus* Kar. & Kir.** Rare; seen only in moist alpine meadow at about 3170 m, along stream east of Kane Lake. 1182.

***Ranunculus pygmaeus* Wahlenb.** Circumpolar. Locally common in moist to wet sites in alpine zone; along rivulets, ledges, and cracks on rock face. 1110, 2315, 2346.

***Ranunculus verecundus* Robins.** Rare in moist alpine boulder field at 3050 m, southwest of Kane Lake. 2345.

Rosaceae

***Potentilla brevifolia* Nutt.** Locally common on dry alpine outcrops at 3050 m, southwest of Kane Lake. 2399.

***Potentilla diversifolia* Lehm. var. *diversifolia*.** Common throughout cirque in moist subalpine and alpine meadows. 2283, 2307, 2372.

***Potentilla fruticosa* L. [*Pentaphylloides floribunda* (Pursh) Löve].** Common on moist ledges and in boulder fields of subalpine and alpine zones; circumboreal. 1171, 2317.

***Potentilla glandulosa* Lindl. var. *pseudorupestris* (Rydb.) Breit.** Local on dry subalpine ledges. 2366.

***Potentilla nivea* L.** Circumpolar. Rare in alpine zone; seen only in moist, sloping meadow at head of waterfall south of Kane Lake. 2379.

***Rubus idaeus* L. var. *gracilipes* Jones.** Common in subalpine boulder fields. 2414.

***Sibbaldia procumbens* L.** Common in alpine and subalpine zones on moist, sandy slopes and ledges; circumboreal. 2288.

Salicaceae

***Salix arctica* Pall. var. *petraea* Andress.** Common throughout cirque in moist subalpine and alpine sites. 2276, 2342, 2376A, 2397; Ertter 2100.

***Salix* sp.** Only vegetative specimens obtained, but appears to be *S. eastwoodiae* Cockerell ex Heller (S. Brunsfeld, University of Idaho, personal communication, 1991). Uncommon in wet subalpine meadow adjacent to the north shore of Kane Lake. 2386.

***Salix nivalis* Hook. var. *nivalis*.** Rare on moist slopes in subalpine and alpine zones. 2337.

***Salix planifolia* Pursh.** Uncommon in subalpine meadow west of Kane Lake. 2266.

***Salix tweedyi* (Bebb) Ball.** Rare; only one robust plant seen at base of small cascade at 2865 m, west of Kane Lake; subalpine zone. 2421.

Saxifragaceae

***Heuchera cylindrica* Dougl. var. *alpina* Wats.** Common in subalpine and lower alpine zones on dry ledges and outcrops and moderately stabilized scree. 2239.

***Lithophragma bulbifera* Rydb. [*L. glabra* Nutt.].** Uncommon on moist subalpine slopes. 2370.

***Mitella pentandra* Hook.** Uncommon in lower alpine and subalpine zones; moist meadows and slopes. 2330.

***Parnassia fimbriata* Common. var. *fimbriata*.** Locally common in moist subalpine and alpine meadows. 1176; Caicco 283.

***Parnassia kotzebuei* Cham. var. *kotzebuei*.** Uncommon and local in gently to steeply sloping alpine meadows and on ledges. 2285, 2328; Caicco 280.

***Saxifraga adscendens* L. var. *oregonensis* (Raf.) Breit.** Uncommon in moist, sloping meadows and talus and along rivulets in alpine zone. 2331; Caicco 282.

***Saxifraga arguta* D. Don [*S. odontoloma* Piper].** Common along streams and rivulets in subalpine and lower alpine zones. 1178, 2335.

***Saxifraga cernua* L.** Uncommon and widely scattered in moist scree and sloping meadows and on ledges of alpine and subalpine zones; circumboreal. 2420.

***Saxifraga debilis* Engelm.** Common on moist and protected alpine ledges and slopes. 1108, 1109, 2324; Caicco 281; Ertter 2105.

***Saxifraga occidentalis* Wats. var. *occidentalis*.** Common in moist subalpine and alpine meadows. 2242, 2277, 2316, 2329, 2401.

***Saxifraga oppositifolia* L.** Common on moist alpine cliff faces; circumboreal. 2358.

Scrophulariaceae

***Castilleja miniata* Dougl.** Common in moist to wet subalpine and low alpine meadows. 2299.

***Mimulus tilingii* Regel var. *caespitosus* (Greene) Grant.** Common along alpine streams and rivulets. 1169.

***Penstemon procerus* Dougl. var. *formosus* (A. Nels.) Cronq.** Common in subalpine zone and uncommon in alpine zone on dry, rocky ledges. 2259.

***Veronica wormskjoldii* Roem. & Schult.** Common in moist to wet alpine and subalpine meadows. 1184, 2295.

Violaceae

***Viola adunca* Sm. var. *bellidifolia* (Greene) Harr.** Common in subalpine and alpine zones on moist meadows and slopes. 2290, 2371.

***Viola macloskeyi* Lloyd var. *macloskeyi*.** Common in wet subalpine meadow adjacent to Kane Lake. 2309.

CLASS LILIOPSIDA

Cyperaceae

***Carex atrata* L. var. *erecta* Boott.** Rare in moist soil of boulder field north of Kane Lake; subalpine. Ertter 2110.

***Carex capillaris* L.** Circumboreal. Uncommon in moist, steeply sloping meadow south of Kane Lake; lower alpine zone. 2332.

***Carex elynoides* Holm.** Uncommon on exposed alpine ledges east of Kane Lake. 2425.

***Carex haydeniana* Olney.** Common in moist subalpine and alpine meadows. 2278, 2431.

***Carex incurviformis* Mack. cf. var. *incurviformis*.** Rare; seen only in one small, steeply sloping, moist meadow at 3353 m, east of Kane Lake. 2411.

***Carex microptera* Mack.** Uncommon in moist subalpine meadows north of Kane Lake. 2383.

***Carex nova* Bailey.** Common in moist alpine meadows. 2291, 2428; Caicco 475.

***Carex phaeocephala* Piper.** Widely scattered in dry alpine sites. 1190, 2430; Ertter 2110A.

***Carex proposita* Mack.** Common on moist subalpine and alpine slopes. 2279.

***Carex rossii* Boott.** Uncommon in dry areas of forest understory. 2247.

***Carex scirpoidea* Michx. var. *pseudoscirpoidea* (Rydb.) Cronq.** Common on moist, sandy subalpine and alpine slopes. 1189, 2254, 2432; Caicco 473.

***Carex scopulorum* Holm var. *bracteosa* Hermann.** Common in wet meadows along creeks and around Kane Lake in subalpine and alpine zones. 2282.

***Carex subnigricans* Stacey.** Uncommon in moist alpine and subalpine meadows. 2429.

Juncaceae

***Juncus drummondii* E. Meyer var. *drummondii*.** Common in moist to dry, sandy soil of subalpine and alpine slopes. 2253, 2297.

***Juncus mertensianus* Bong.** Common in moist alpine meadows. 1195.

***Luzula parviflora* (Ehrh.) Desv.** Common in moist subalpine and low alpine meadows. 2320.

***Luzula spicata* (L.) DC.** Common on moist, unstable slopes of subalpine and alpine zones; circumboreal. 1197, 2323; Caicco 480; Ertter 2103.

Liliaceae

***Allium brandegei* Wats.** Rare in dry forest opening north of Kane Lake. 2394.

***Allium brevistylum* Wats.** Common in moist, steeply sloping meadows in subalpine and lower alpine zones. 2334.

***Calochortus eurycarpus* Wats.** Rare in dry areas of subalpine meadow north of Kane Lake. 2384.

***Zigadenus elegans* Pursh.** Common in moist, sloping alpine meadows. 2340; Caicco 478.

Poaceae

***Agropyron scribneri* Vasey [*Elymus scribneri* (Vasey) Jones].** Uncommon on dry, unstable alpine and subalpine slopes. 2272.

***Agrostis humilis* Vasey.** Uncommon on moist, sandy alpine ledges. 1196, 2368.

***Agrostis variabilis* Rydb.** Uncommon in moist alpine meadows. 1194.

***Calamagrostis purpurascens* R. Br.** Uncommon on dry, rocky subalpine and alpine ledges. 2365.

***Danthonia intermedia* Vasey.** Locally common in subalpine meadows north of Kane Lake. 2389.

***Deschampsia cespitosa* (L.) Beauv. var. *cespitosa*.** Common throughout cirque in subalpine and alpine moist meadows where it is often dominant; circumboreal. 1192, 2325; Caicco 481.

***Festuca idahoensis* Elmer var. *idahoensis*.** Uncommon in dry forest openings north of Kane Lake. 2241.

***Festuca ovina* L. var. *brevifolia* (R. Br.) Wats. [*F. brachyphylla* Schult. & Schult.].** Uncommon in alpine zone; moist to dry meadows and ledges. 2273, 2407.

***Oryzopsis exigua* Thurb.** Common in dry subalpine sites north of Kane Lake. 2251.

***Phleum alpinum* L.** Common in wet to moist subalpine and alpine meadows; circumboreal. 1191, 2281.

***Poa alpina* L.** Common in wet to moist subalpine and alpine meadows. 2296.

***Poa cusickii* Vasey var. *cusickii*.** Uncommon in moist to dry subalpine meadows. 2296.

***Poa cusickii* Vasey var. *epilis* (Scribn.) Hitchc.** Uncommon in moist subalpine meadows. 2382.

***Poa gracillima* Vasey.** Uncommon on dry ledges in forest openings. 2238.

***Poa incurva* Scribn. & Will.** Uncommon in dry subalpine meadows. 2381.

***Poa interior* Rydb.** Uncommon on dry alpine slopes and in scree. 2426.

***Poa nervosa* (Hook.) Vasey var. *wheeleri* (Vasey) Hitchc.** Common on dry ledges and in forest understory north of Kane Lake. 2234.

***Poa rupicola* Nash.** Uncommon on dry, rocky alpine slopes. 2427.

***Sitanion hystrix* (Nutt.) Smith var. *hystrix* [*Elymus elymoides* (Raf.) Swezey].** Uncommon in subalpine and alpine zones on dry, rocky ledges and slopes. 2243.

***Trisetum spicatum* (L.) Richter.** Circumboreal. Common in alpine and subalpine zones; moist meadows and ledges. 2280.

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LAKEWARD AND DOWNSTREAM MOVEMENTS OF AGE-0 ARCTIC GRAYLING (*THYMALLUS ARCTICUS*) ORIGINATING BETWEEN A LAKE AND A WATERFALL

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ABSTRACT.—Arctic grayling in Deer Lake, Montana, spawn only in the 350-m segment of outlet stream between the lake and a waterfall. The purpose of this study was to examine consequences of and possible adaptations by this population to spawning above the falls, by determining the extent of loss over the falls of age-0 young, the daily and seasonal patterns of such losses, and the seasonal pattern of movement upstream into the lake by the remaining young. We measured fish movements during 1989 and 1990 with traps placed at the outlet and at the falls, from fry swimup in July until October or November. Young went over the falls predominantly as newly swimming fry at night. In 1989 about 5000–9000 were lost downstream, representing an estimated 4–7% or less of young produced. Most young thus appear adapted to maintaining their position above the falls. A few started entering the lake in August and September, but only 95 in 1989 and 23 in 1990 had done so by the time observations were ended by the onset of wintery conditions. Most movement into the lake appeared to occur sometime during the six to seven months of annual ice cover. This extended period of stream residence contrasts with early lakeward movements reported for other inlet-spawning, lacustrine grayling populations and may be an adaptation for avoiding predation by large conspecifics in Deer Lake.

Key words: migration, fish, grayling, Thymallus arcticus, *salmonids, waterfall, stream, lake.*

Limited information is available on movements of young fish from populations inhabiting or spawning in small headwater streams above waterfalls. An innate tendency of young fish from such populations to hold position or move upstream in water current (positive rheotaxis) would be highly advantageous in preventing their irretrievable loss over the falls. Such loss should be limited to enable the population to maintain itself, and appropriate behavioral adaptation would be promoted through removal from the gene pool of young fish that did go downstream. Evidence for such adaptation is provided by studies reporting little or no loss over waterfalls of young fish from long-established, native populations of rainbow trout (*Oncorhynchus mykiss*) and cutthroat trout (*O. clarki*) in North America (Northcote 1969, Northcote and Hartman 1988) and brown trout (*Salmo trutta*) in Europe (Jonsson 1982). Experimental studies have provided evidence for a genetic basis of such rheotactic adaptation in rainbow trout and brown trout (Northcote 1981, Northcote and Kelso 1981, Jonsson 1982).

Although there is evidence for genetically based, positive rheotaxis by young Arctic grayling (*Thymallus arcticus*) in streams (Kaya 1989, 1991), there have been no previous studies on their possible loss over waterfalls. Young grayling may be more susceptible to such loss than young trout, since young grayling are much smaller and appear to be weaker swimmers. At swimup (initiation of swimming), young grayling are about 9–11 mm in length (Kaya 1991), compared to 20 mm or more for rainbow trout (Northcote 1962). The present observations were conducted on a population of grayling that lives in a lake near the head of a mountain valley and spawns only in a short stream section between the lake outlet and a waterfall. Objectives of the study were to determine whether age-0 (first-year) young are lost downstream over the falls, the daily and seasonal patterns of such losses, and the seasonal patterns of their upstream movement into the lake. Perpetuation of such a population would depend on limited downstream loss of their progeny, and residence in the lake would require upstream migration by the young. The study was designed to include movements of the earliest mobile larvae, an aspect that appears lacking from most past studies involving downstream movements from salmonid populations above waterfalls.

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STUDY SITE AND POPULATION

Observations were conducted in 1989 and 1990 on the 350-m long section of Deer Creek that flows from Deer Lake to a 3-m, vertical waterfall. The lake is located at 2780 m altitude near the head of a mountain valley in the Madison Range of southwest Montana. Dimensions of the stream on 19 August 1990, measured bank-to-bank at five locations along each of 34 transects between the lake outlet and the waterfall (Deleray 1991), were mean width of 5.88 m (range 1.08–21.0), mean depth of 0.10 m (range 0.0–0.41), and mean water velocity (measured at 0.6 × depth at each location) of 0.05 m/sec (range 0.0–0.48). Estimated discharge volume ranged from about 0.02 to 0.05 m^3/sec between 2 July and 9 September 1990.

Previous observations had indicated that Arctic grayling, the only fish in the lake, spawn only in the outlet stream (Kaya 1989). The outlet stream is inhabited by grayling fry (age-0 fish smaller than about 2.5 cm in length; Piper et al. 1982) and other young up to about 14 cm in length. Larger fish are rare, except when spawning adults are present during early summer. Numbers of adults spawning in the stream were estimated by electrofishing mark-and-recapture methods at 803 (95% CL ±104) in 1989 and 1109 (95% CL±124) in 1990, with similar numbers of males and females (Deleray 1991). The 350-m segment between the lake and the waterfall is the only part of Deer Creek inhabited by grayling. Near the base of the waterfall the stream disappears beneath the surface of a steep talus slope before reemerging about 200 m downslope. Grayling are not present in the 10 km of stream between the lake and the Gallatin River, perhaps because of the stream's steep gradient (about 1000 m/10 km) and numerous cascades. Fish habitat is absent upstream from the lake, and the population is thus physically isolated within the lake and the short section of stream above the waterfall.

METHODS

Methods and observation schedules were influenced by the relatively remote location of the study site. The lake is located within a designated wilderness area and is reached via a trail that extends about 10 km from and climbs about 1000 m above the nearest motor vehicle access. Loss of ice cover from the lake and stream and spawning activities by grayling were monitored through weekly hikes to the site starting in late May. Observations of fish behavior started as the ice thawed and adults began entering the stream, mid-June in 1989 and late June in 1990, and ended as ice started forming on the lake and stream margins (10 November 1989) or as snow accumulations on the trail made access difficult (11 October 1990). Stream temperature was continuously recorded throughout both observation seasons with a Peabody Ryan Model D thermograph placed about 30 m downstream from the lake. Daily mean temperature was calculated as the average of daily maximum and minimum.

Traps with 1-mm-mesh netting were placed to determine the dates fry became free-swimming, and to monitor their movement downstream and upstream out of the outlet stream. In 1989 three fry emergence traps (45 × 45 cm) of the type described by Fraley et al. (1986) were placed over the substrate after most spawning had ceased, over areas where fish had been seen spawning and where concentrations of eggs were visible. Because Arctic grayling spawn over the substrate without excavating redds, eggs were readily visible among the substrate particles. One emergence trap was placed in a spawning area about 30 m below the outlet, and the other two were placed in the principal spawning area about midway through the stream length. Swimup fry in the traps were removed and tabulated daily or on alternate days until emergence ceased.

One-way traps were placed across the lake outlet and at the top of the waterfall to monitor movement of young out of the stream. The upstream trap had V-shaped, screened barriers extending completely across the outlet and leading upstream into a holding box. This trap retained fish as they entered the lake. The trap was installed after most adult spawners had left the stream but before the young became free-swimming. After installation, the trap was in continuous operation through both observation seasons. It was inspected at intervals varying from several days to about one week; young were removed, measured, and released upstream into the lake.

The downstream trap was a drift net with its

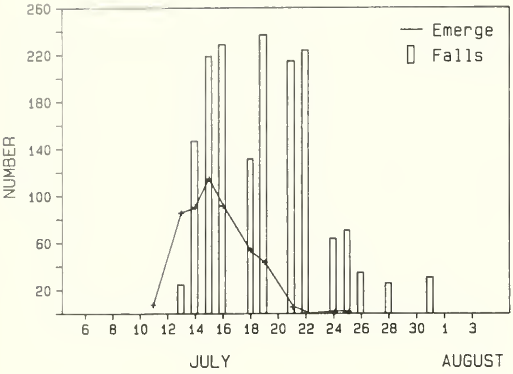

Fig. 1. Total number of young Arctic grayling (*Thymallus arcticus*) in three emergence traps placed over the substrate, and in the waterfall trap, Deer Creek, Montana, 1989.

opening positioned at the lip of the waterfall; it collected young that were going over the falls. In 1989 this trap sampled about 0.3–0.5 of the stream volume, as estimated by comparing flow rate into a plastic sack attached to the trap versus estimated stream discharge volume. In 1990 V-shaped barriers were added to direct all flow through the net. In 1989 the trap was installed on sampling days and left in place for about 24 h before the young within were tabulated and measured. The trap was deployed on 6 July, before fry became free-swimming, and operated at intervals of one to two days until numbers in the trap declined sharply. Thereafter, the trap was operated at intervals of several days to two weeks until 19 October. In 1990 this trap was operated less frequently, at intervals ranging from five days during the swimup period to about four weeks in September and October, to determine diel patterns of movement over the falls of young at different ages post-swimup. Sampling began on 23 July as fry started to swim. On sampling dates the trap was deployed at 1000 or 1100 h (Mountain Standard Time); the trap was emptied of young at 1400 h, and thereafter every 4 h until 1000 h the next day.

RESULTS

Spawning occurred through much of the 350-m length of the stream, from about 10 m below the lake outlet to within 15–20 m of the falls. The most heavily used area was a 10-m reach about 130–140 m above the falls. In 1989 spawning occurred during the last week of June, and swimup of fry in the emergence traps began about 11 July, peaked in mid-month, and continued until about 25 July (Fig. 1). Spawning in 1990 occurred during the first week in July, and swimup of fry began in mid-month and continued to the end of the month.

In 1989 fry started appearing in the falls trap as they became free-swimming (Fig. 1). Highest daily totals of fry in the falls trap, generally over 200 per day, occurred 15–22 July as numbers of fry becoming free-swimming in the emergence traps peaked, and then declined. The swimup period ended about 25 July; thereafter, within a week, numbers of young in the falls trap declined to 0–6 per day. No young entered the falls trap after 20 September.

Movement of fry over the falls was concentrated within a 19-day period, 13–31 July. The falls trap was operated for 13 of these days, and the mean number of fry per 24-h sample was 127.3. Extrapolation from the estimated 30–50% of total stream volume that passed through the net, and application of the 13-day mean to 19 days, yielded a crude estimate of 4837–8062 young grayling lost over the falls 13–31 July. Numbers in the falls trap averaged only 2.7 per day during the 11 days sampled from 1 August to 20 September, the last day young entered the trap. Similar extrapolation to this 51-day period yielded a crude estimate of an additional 275–459 young lost. Thus, the number of young lost downstream over the falls in 1989 during the period from swimup of fry to onset of ice cover over the stream was roughly estimated at 5000–9000.

Fry were already becoming free-swimming when the falls trap was installed on 23 July 1990. Numbers of young per day in the falls trap peaked at 561 on 28 July, diminished to 49 ten days later on 6 August, and to 5 by 8 September. No young entered the trap on 12 October, the last day sampled in 1990. During the swimup period fry went over the falls predominantly at night (23 and 28 July; Fig. 2). However, there was no consistent pattern of diurnal vs. nocturnal movement among the fewer young fish that went over the falls on later dates (6 and 17 August; Fig. 2). Too few days were sampled at the falls in 1990 to estimate total numbers lost.

In contrast to early losses over the falls, upstream movement of young grayling into the lake did not begin until late summer, when the fish were larger and water temperatures were cooling (Fig. 3). Small numbers of young were trapped at the lake outlet starting in mid-August

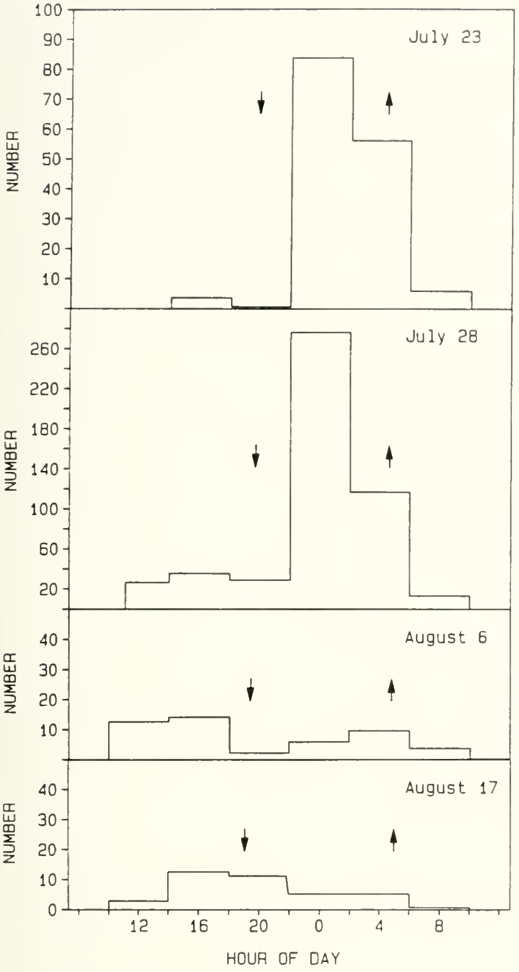

Fig. 2. Diel pattern of young Arctic grayling (*Thymallus arcticus*) accumulated in waterfall trap during 3- or 4-h sampling periods (1000 or 1100 h to 1400 h, then at 4-h intervals thereafter), Deer Creek, Montana, 1990. Note change of y-axis on July 28. Mean sizes of young on these sampling dates are in Figure 3. Arrows indicate sunset and sunrise.

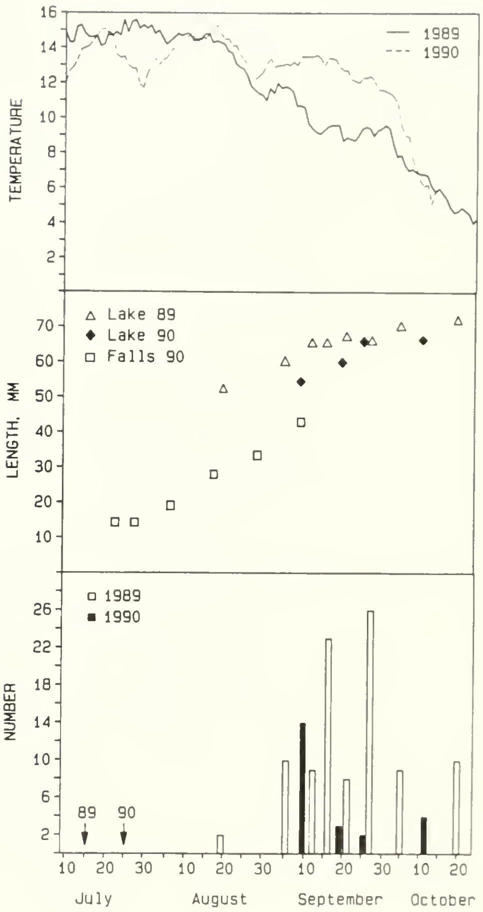

Fig. 3. Mean daily temperature (°C) of Deer Creek, Montana, mean total lengths of age-0 grayling (*Thymallus arcticus*) in waterfall and lake traps, and numbers of age-0 grayling in the lake trap, 1989 and 1990. Arrows indicate dates when numbers of young becoming free-swimming (collected in emergence traps) peaked during 1989 and 1990.

1989 and early September 1990. Total numbers of young trapped per 3-day to 1-week periods in September and October were 0–26 in 1989 and 0–14 in 1990 (Fig. 3). Only 95 age-0 young had moved up into the lake in 1989 and 23 in 1990, before observations were terminated by the onset of winterlike conditions in November 1989 and October 1990. While age-0 grayling in the falls trap were mostly newly swimming fry that averaged 12–14 mm in length, the smallest moving upstream into the lake trap averaged 52–54 mm in length (Fig. 3).

Although numbers of resident young in the stream were not estimated, visual observations indicated that age-0 fish were abundant in November 1989 as ice was starting to form on the stream, but were present in much fewer numbers (as age-1 fish) when ice cover melted the following June. The age-1 fish still in the stream in June 1989 and 1990 had upstream patterns of movement similar to those of the age-0 fish; very few entered the lake during the June–November study period, and these limited upstream movements occurred mostly between early September and the end of observations in October or November. In 1989 only seven age-1 fish were in the lake trap from June to the end of August, and 38 more from September to the end of observations in November. In 1990 only two age-1 fish were trapped, both in September. Age-1 fish were nearly absent from the falls trap; three were trapped in 1989 and two in 1990. Fish older than age-1 were rare in the stream when ice cover thawed in June of both years.

During the summer of 1990, six adults remained in the outlet stream. These fish were seen in shallow water (5–10 cm deep) chasing groups of young in late July. One was captured with a dip net and had 12 age-0 grayling in its stomach.

DISCUSSION

Since we did not estimate the number of young produced in the stream, we do not know the percentage of total young lost over the falls between swimup and the end of observations in October and November. Two considerations suggest that the losses represented a relatively small percentage of young produced. First, it was visually apparent that age-0 young remained abundant and widely distributed throughout the stream until the end of each observation season. Second, we estimated that the number of eggs that could have been spawned by this population during 1989 was about 1.3 million. This was based on the estimated average of 2988 eggs in each of seven females sampled (range 2459–3674) and the estimated number of 426 adult females in 1989 (Deleray 1991). If we assume, as an example, that swimup fry resulted from 10% of this potential egg deposition, then the estimated loss of young over the falls (5000–9000) would be about 4–7% of fry produced in 1989. We do not know of any estimates of the relationship between potential egg deposition and actual fry production by grayling. However, a figure of 10% seems conservative compared with recent estimates of 11.5–22.2% for chum salmon (*Oncorhynchus keta*) and 16.4–29.1% for coho salmon (*O. kisutch*) in a Canadian stream, with the lower percentages associated with poor substrate quality (Scrivener and Brownlee 1989).

The grayling lost downstream were predominantly small, newly swimming fry that went over the falls at night. The nocturnal downstream movement of the young was similar to those of young from inlet-spawning populations of grayling (Kruse 1959, Lund 1974, Wells 1976) and other salmonids (McCart 1967, Northcote 1969, Brannon 1972). These observations were also consistent with results of experiments in an artificial stream (Kaya 1989), which indicated that although young Deer Lake grayling had an innately greater tendency to swim upstream than those of an inlet-spawning population, many moved downstream, especially in darkness.

If loss over the falls results from deliberate downstream migration by the young, then this may indicate that the Deer Lake population has not yet completely adapted to outlet spawning. If so, then the waterfall is continuing to act as a selective factor removing those young with inappropriate responses. Incomplete adaptation has also been suggested as an explanation for downstream movement by many swimup fry of rainbow–cutthroat hybrid trout that spawn in the outlet of a Colorado lake (Lentsch 1985). The lake had first been planted with trout about 100 years earlier. Little or no downstream loss has been reported from populations of brown and rainbow trout native to waters above falls (Northcote 1969, 1981, Jonsson 1982, Northcote and Hartman 1988), in contrast to downstream movement over cascades of an estimated 22% of marked rainbow trout in a stream that had been stocked repeatedly in preceding years with nonnative rainbow trout (Chapman and May 1986). The Deer Lake population almost certainly originated through a transplant of young from an inlet-spawning population sometime during the present century. In Montana, grayling were not present above natural barriers to upstream movement, and the only lakes within the original range that were naturally accessible to fish and known to have contained native grayling were Upper and Lower Red Rock lakes and perhaps Elk Lake, of the Red Rock River drainage (Nelson 1954, Vincent 1962). Another lacustrine population originated with the creation of Ennis Reservoir on the Madison River, which contained native grayling. The Red Rock, Elk, and Ennis populations are inlet-spawning. Populations in other lakes originated through stockings that began after artificial culture of the species was initiated in 1898 (Henshall 1906). Unpublished records of regional, state, and federal hatcheries involved in these stocking programs indicate that fertilized eggs were obtained from Upper Red Rock

Lake or Ennis Reservoir or other inlet-spawning populations established through transplants from these two sources (Kaya 1989, 1990). Outlet-spawning populations are known to have evolved elsewhere from transplants of inlet-spawning grayling (Kruse 1959) and rainbow trout (Northcote 1969).

It is possible that downstream loss of many young fish occurs even from populations well adapted to spawning above a waterfall. With native, above-falls populations that have been studied, the young sampled were brown trout from about 10 cm to over 20 cm in length (Jonsson 1982), or rainbow and cutthroat trout whose sizes were not stated (Northcote 1969, 1981, Northcote and Hartman 1988). Given the rapid post-swimup decline of downstream movement observed in the present study, conclusions on magnitude of such losses would have been very different if the sampling had begun one or two weeks after the end of the swimup period, or if the only fish sampled were larger than 1.5–2.0 cm.

Factors other than deliberate downstream movement could have produced losses over the falls, including passive drift or local dispersal. Those young that were lost could have originated from eggs either spawned within or drifted to locations close to the falls. Adults spawned within 15–20 m above the falls, and we confirmed visually that many eggs drift downstream from spawning areas after being broadcast over the substrate. Fry originating from eggs near the falls could be lost through passive drift if they became free-swimming at night and were consequently displaced downstream in the darkness, as has been described of European grayling (*T. thymallus;* Bardonnet and Gaudin 1990). Downstream losses could also represent passive drift of dead or unhealthy fish, as suggested by a report that 81% of young brown trout produced in a section of stream did not survive and drifted downstream, mostly at night (Elliott 1986). We did not attempt to determine the health of young grayling in the falls trap.

Loss over the falls could be an indirect consequence of local dispersal of young within the stream as they became free-swimming. Young sockeye salmon (*Oncorhynchus nerka*) of outlet-spawning populations have been reported to temporarily disperse downstream before holding position or swimming upstream into lakes (McCart 1967, Brannon 1972). Young grayling in Deer Dreek also disperse locally from the immediate spawning areas, some of them apparently downstream. For those becoming free-swimming near the falls, even localized downstream dispersal could result in some being carried over, especially under conditions of poor visibility at night.

The results indicate that Deer Lake grayling spend at least the first, and possibly also their second, summer and early to mid-autumn in the outlet stream. However, the results did not permit us to determine the exact timing of most movement by young into the lake, or whether they move upstream predominantly as age-0 or as age-1 fish. The very few young that moved into the lake during both observation seasons could not account for the numbers of spawning adults produced in the population. Since there is no other source of young, and since the 1989 observation season extended over the entire ice-free period on the stream, maintenance of the Deer Lake population must depend on upstream movement of young sometime during the six to seven months of annual ice cover. Although age-0 young greatly diminished in numbers and age-1 fish virtually disappeared from the stream between the onset of ice cover in November 1989 and its thawing in June 1990, we do not know the proportions of these reductions in numbers attributable to movement into the lake, death, or loss over the falls. The greatly diminished numbers of young in the falls trap during late summer and their absence in the trap by October of both years suggest that downstream losses during winter may be small. The chronology of major movement by young grayling into the lake and the numbers and ages of fish involved would need to be resolved by observations during winter.

Little is known about duration of stream residence for outlet-spawning populations of Arctic grayling. Young from inlet-spawning populations of the species typically have an early descent to the lake, ranging from immediately after swimup (Kruse 1959, Lund 1974, Wells 1976) to within several weeks (Nelson 1954). We are not aware of other studies on stream residence times of young grayling from outlet-spawning populations and so do not know whether extended period of stream residence is typical for such populations. Young rainbow trout of outlet-spawning populations tend to remain for extended periods of at least a month to a year or more before migrating upstream to lakes, while those of inlet-spawning populations migrate when newly swimming in some populations and after extended periods of stream residence in others (Northcote 1969). The extended stream residence of young Deer Lake grayling is also consistent with their lesser tendency to swim upstream in an artificial stream as early fry (from swimup to three weeks), compared with their responses when older, within a study period of up to 10 weeks post-swimup (Kaya 1989, 1991).

It may be that young of an outlet-spawning population need to attain larger sizes and thereby become stronger swimmers before they can swim upstream into the lake. However, this possibility appears contradicted by our casual observations that age-0 grayling of all sizes in Deer Creek, starting from those newly swimming, were capable of swimming upstream when they were disturbed by our presence. Those young originating from spawning areas within a few meters of the lake outlet could have entered the lake by moving only a short distance upstream.

Another possible factor, quality of rearing habitat, also does not appear to favor extended residence in Deer Creek. Deer Lake grayling grow slower during their first two years than those of other lacustrine populations studied thus far in Montana, but thereafter they grow at similar or faster rates (Deleray 1991). Unlike young Deer Lake grayling, those from inlet-spawning populations in Montana spend their first summer and autumn growing season in lakes. The slower early growth of Deer Lake grayling thus appears related to their spending their first growing seasons in the stream rather than in the lake.

We speculate that young Deer Lake grayling may remain in the outlet stream to avoid intraspecific predation in the lake. Eriksen (1975) observed that age-0 grayling in several Montana lakes occupied shallow, near-shore areas among rooted aquatic vegetation, and suggested that their distribution provided protection against predation by the adults. Behavior of the few post-spawning adults that remained in Deer Creek during the summer of 1990 confirmed that adults will prey on the young. Young grayling would likely be susceptible to predation by larger conspecifics in Deer Lake because of its high water clarity throughout the summer and the lack of rooted macrophytes. In the outlet stream the only potential predators of young grayling that we saw were the relatively few residual adult and age-1 grayling remaining through the summer, and an occasional belted kingfisher (Aves, *Ceryle alcyon*). Thus, the movements of age-0 Deer Lake grayling that remain in the outlet stream appear adapted both to beginning their existence a short distance above a waterfall and to avoidance of predation by larger conspecifics in the lake.

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EFFECTS OF BROWSING BY MULE DEER ON TREE GROWTH AND FRUIT PRODUCTION IN JUVENILE ORCHARDS

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ABSTRACT—The effects of big game depredation on juvenile fruit trees were studied in northern Utah. Utilization of trees was determined by counts of nipped and intact buds in spring. Height, width, basal diameter, number of buds, and initial fruit production of peach and apple trees were determined from trees protected from or browsed by mule deer in winter. Results from the 10 orchards studied indicated that removal of buds at the observed browsing levels had no effect on tree growth or initial fruit production.

Key words: depredation, mule deer, orchards, fruit trees, deer damage evaluation, apple trees, peach trees, winter browsing.

Whenever depredation occurs in commercial orchards, potential crop losses due to big game browsing become a major concern to growers. Browsing of juvenile fruit trees has important economic consequences because the effects may limit future crop production and increase tree mortality. Research has clearly shown that browsing by big game on mature apple trees causes significant crop loss within the browsing zone (Katsma and Rusch 1979, 1980, Austin and Urness 1989). However, limited information on the effects of browsing on juvenile fruit trees is extant.

Westwood (1978) suggested deer browsing may be especially damaging to young trees, but rarely would browsing be expected to cause mortality. Harder (1970) reported no differences in trunk diameter growth between protected and unprotected apple trees with one winter of bud-removal browsing by mule deer. In this Colorado study of 160 trees, no mortality was attributed to bud-removal browsing, although 8 trees died as a result of bark damage caused by antler rubbing. Similarly, McAninch et al. (1985) in a New York study reported 9 of 10 growth parameters measured between protected and browsed trees showed no significant differences. One parameter, basal diameter, was smaller on browsed trees. However, this study with white-tailed deer also showed that average diameters of browsed limbs appeared greater than protected limbs, suggesting possible growth stimulation as a result of deer browsing.

In our project only bud-removal browsing was studied, and since browsing during summer was negligible, we considered only overwinter depredation. The purpose of this study conducted in northern Utah was to measure the degree of browsing in young fruit trees and to assess the browsing effects on tree growth and initial crop production.

METHODS

The percentage of buds browsed by mule deer was determined in March, during late dormancy, after deer switched diets from winter browse to herbaceous spring growth (Kufeld et al. 1973, Austin and Urness 1983). Percent bud removal was determined by counting all intact and nipped buds and then dividing nipped buds by the total nipped plus intact buds. Nipped buds are easily identified by the exposed and broken woody twigs (Katsma and Rusch 1979). Counted intact buds were restricted to terminal buds of the previous summer's annual growth, and all protruded buds along second-year and older stems >1 cm in length (Austin and Urness 1987). Protruded was defined by visualizing a perpendicular line from the twig to the tip of the bud, and an observable space was required between the line and the bud-twig intersection.

Tree growth measurements were taken after the end of the growing season but before winter browsing occurred. Tree height was measured to the nearest 1.0 cm from ground level, tree width to the nearest 1.0 cm at the height where maximum width occurred. Width was measured in north-south and east-west directions and the mean recorded. Basal trunk diameter was measured to the nearest 0.1 cm using dial calipers at 10 cm above the graft scion. Diameter was similarly measured on north-south and east-west directions and the mean recorded. The number of intact buds, using the same definition as that for bud-removal determinations, was counted using hand-tally registers. Where harvestable crops were produced, all fruits were hand-picked and counted. Specific methods are reported in the results for each orchard.

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Data were analyzed between protected and browsed trees and between trees with various intensities of browsing, using the standard t test of the means. Confidence level was set at $P \leq .05$.

RESULTS

Orchard 1

A 4 × 6 block of 24 equal age and size Elberta peach trees, planted in spring 1986, was selected for study. Alternating trees, determined by coin toss, were fenced during three winters, 1986–89. During the fourth winter, 1989–90, all trees were fenced. Because within-year browsing effects decrease fruit production (Katsma and Rusch 1980, Austin and Urness 1989), trees were protected from browsing to compare production between previously browsed and protected trees. Tree measurements were taken, and peaches were hand-picked and counted in late summer 1990, the first year of commercial harvest.

Percent bud removal as measured in spring 1987, 1988, and 1989 was 35.6, 76.6 and 73.5%, respectively. Even with this high degree of browsing by deer, trees fully recovered during the summer growing seasons. No differences between protected and browsed trees were found for any tree measurements or fruit production (Table 1).

Orchard 2

A small commercial orchard comprising 210 Elberta peach trees was planted in spring 1986. Percent overwinter bud removal was determined in early spring 1987. Since 9 trees showed bark scraping damage, they were deleted from the sample. Trees were placed into three equal groups of 67 by the percentage of bud-removal browsing damage: heavy 61–100%, moderate 34–60%, and light 0–33%. Tree measurements were made following the 1987 summer growing period. No differences in tree measurements were found among the three intensities of browsing by mule deer (Table 1).

Orchard 3

Twelve pairs of equal age and size Yellow Delicious apple trees were carefully selected by ocular observation within a commercial orchard planted during spring 1984. One tree of each pair, determined by coin toss, was protected from browsing by fencing during five winters, 1984–89. During the sixth winter, 1989–90, for the same reason as described for orchard 1, all trees were fenced.

Percent bud removal from browsing was 76.4, 60.5, 41.7, 23.6, and 63.2% for years 1985–89, respectively. No differences between protected and browsed trees were found for any tree measurements or fruit production (Table 1).

Orchard 4

Twelve pairs of equal age and size Red Delicious apple trees were carefully selected by ocular observation within a commercial orchard planted in spring 1983. One tree of each pair, determined by coin toss, was protected from browsing by fencing during three winters, 1984–87. During winter 1986–87 a deer-proof fence was constructed around the orchard, and, consequently, deer use was close to zero (0.4%). During the two previous winters (1984–86) percent bud removal was 71.0 and 17.0%, respectively. No differences between protected and browsed trees were found for either tree measurements or number of fruits (Table 1). Also, flower cluster counts, which were collected in spring 1987 as part of an ongoing parallel study (Austin and Urness 1987), showed no difference between protected ($x = 166$) and browsed ($x = 169$) trees.

Orchard 5

Twelve pairs of equal age and size Red Delicious apple trees were selected within a commercial orchard planted in spring 1985. One tree of each pair, determined by coin toss, was protected from browsing during four winters, 1985–1989. During the fifth winter, 1989–90, all trees were fenced.

TABLE 1. Mean growth measurements and initial fruit production from juvenile peach and apple trees protected from or browsed by mule deer in winter.

					Mean tree measurements					
Orchard No.	Fruit tree	Treatment	N	Years	% buds removed	Height (cm)	Width (cm)	Basal diameter (mm)	No. of buds	No. of fruits
1	Elberta peach	Browsed	12	1986–90	62	225	257	5.6	—	104
		Protected	12			230	247	5.7	—	103
2	Elberta peach	Heavily browsed	67	1986–87	61–100	120	88	2.6	61	—
		Moderately browsed	67		34–60	124	92	2.7	67	—
		Lightly browsed	67		0–33	122	91	2.7	65	—
3	Yellow Delicious apple	Browsed	12	1984–90	53	192	136	5.1	250	72
		Protected	12			193	149	5.2	238	70
4	Red Delicious apple	Browsed	12	1984–87	44	569	248	4.4	349	75
		Protected	12			588	262	4.4	375	59
5	Red Delicious apple	Browsed	12	1985–90	24	259	163	5.4	577	3
		Protected	12			250	158	5.4	570	3
6	Golden Delicous apple	Heavily browsed	20	1987	65–92	198^a	93^a	3.5	96	—
		Moderately browsed	20		28–64	192^a	88	3.5	93	—
		Lightly browsed	20		0–27	175^b	80^b	3.5	92	—
7	Red Delicious apple	Heavily browsed	8	1985–86	49	88	22	1.7	11	—
		Moderately browsed	8		21	98	30	1.8	10	—
		Protected	8			92	21	1.6	7	—
8	McIntosh apple	Heavily browsed	8	1985–86	50	132	62	2.4	31	—
		Moderately browsed	8		35	126	47	2.1	22	—
		Protected	8			129	44	2.6	17	—
9	Jonathan apple	Heavily browsed	8	1985–86	28	147	69	2.4	26	—
		Moderately browsed	8		22	123	48	2.0	22	—
		Protected	8			131	69	2.0	45	—
10	Red Delicious apple	Browsed	12	1985–87	39.4	167	67	5.1	90	—
		Protected	12			159	63	5.0	107	—

[1] Figures with different superscripted numbers within columns were significantly different. $P \leq .05$

Percent bud removal from browsing was 16.7, 0.0, 16.7, and 61.0 for years 1985–89, respectively. No differences between protected and browsed trees were found for any tree measurements or fruit production, which was greatly reduced in 1990 due to cold temperatures in spring (Table 1).

Orchard 6

A 2 × 30 block of 60 two-year-old Golden Delicious apple trees was measured for overwinter bud-removal browsing use in spring 1987. Utilization during the previous winter was unknown, but was probably similar to the use measured in 1987. Percent bud removal ranged from 0 to 92%, with a mean of 46.7% (Table 1). Trees were placed into three groups of 20 by bud-removal classes: 0–27, 28–64, and 64–92%. Surprisingly, heavily and moderately browsed trees had significantly greater height at the end of the growing season than lightly browsed trees, and heavily browsed trees also had greater width than lightly browsed trees (Table 1). Although other factors, such as pruning, could have accounted for these increases, height and width may have been increased by browsing. No differences were found in basal diameters or number of buds.

Orchards 7, 8, 9

Twenty-four equal age and size trees of Red Delicious, McIntosh, and Jonathan apples were planted in spring 1985 for this study. In winter 1985–86, one-third (8 of each species) of the trees, randomly selected, were protected; one-third received moderate browsing by tame mule deer as modified by temporary fencing; and one-third received heavy browsing. Mean bud removal varied from 21 to 35% under moderate browsing, and 28 to 50% under heavy browsing (Table 1). Following the summer growing season in 1986, no significant growth differences in tree measurements were found between protected, moderately browsed, or heavily browsed trees (Table 1).

Orchard 10

Twelve pairs of equal age and size Red Delicious apple trees were selected within a commercial orchard planted in spring 1983. One tree of each pair, determined by coin toss, was protected from browsing during winters 1985–87. Percent bud removal from browsing was 76.6, 37.4, and 4.1%, respectively. No differences between protected and browsed trees were found (Table 1).

DISCUSSION

Percentages of bud removal measured from these 10 orchards were mostly less than 65%. Browsing by mule deer during winter dormancy at this level of use was not sufficient to cause a decrease in tree growth parameters measured. From the view of carbohydrate reserves, decreased productivity would not be expected if the total number of intact buds available for spring growth were sufficient to maintain balance with the root system. This was the observed case.

In this study trees were not browsed severely. As a suggested definition, severely browsed trees would include browsing of >90% of the available protruded buds, removal of >70% of the current annual growth, scraped bark on the central leader and/or scraped bark on two or more primary branches, or limb breakage. Certainly, as the level of browsing increases toward severe levels, the potential for permanent damage and reduced growth also increases. The level of browsing intensity needed to damage juvenile fruit trees is unknown, but it is apparently higher than that which occurs in most depredation situations in northern Utah and elsewhere (Harder 1970, McAninch et al. 1985).

The intensity of browsing needed to cause measurable damage would also be expected to vary with the quality of the horticultural practices involved in managing the orchard. In this study all orchards received high-intensity care, including adequate irrigation, periodic spraying, weed control, etc. Orchard trees receiving lower intensities of care and increased environmental stress from pests, or competition from weeds, may respond negatively to similar levels of deer browsing.

In conclusion, the results from this study of juvenile apple and peach fruit trees were consistent with previous research (Harder 1970, McAninch et al. 1985). Browsing by mule deer at the intensities observed had no negative effects on tree height, width, basal diameter, number of buds, or initial fruit production.

ACKNOWLEDGMENTS

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CHANGES IN RIPARIAN VEGETATION ALONG THE COLORADO RIVER AND RIO GRANDE, COLORADO

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ABSTRACT.—Changes in vegetation including area occupied, canopy cover, and maturity class of cottonwoods (*Populus* spp.) within lower-elevation zones of the Colorado River and Rio Grande in Colorado were monitored over 25- and 37-year intervals, respectively, using photo-interpretative methods. Estimated loss of cottonwoods along the Colorado River was 2 ha/km (−17.5%), and remaining stands had become more open and older. Cottonwoods along the Rio Grande increased 1.6 ha/km (9.3%) with minor canopy cover and maturity class changes. Area occupied by shrubs and river channel changed little along the Colorado River, but declined along the Rio Grande. Loss of hay meadow occurred along both rivers, whereas developed land increased along the Colorado River and farmland increased along the Rio Grande. Wildlife habitats along the Colorado deteriorated much more rapidly than those along the Rio Grande during monitored intervals.

Key words: riparian, Colorado, inventory, cottonwood, Populus *spp., wildlife habitat*

Riverine systems in the Great Basin and southwestern United States are important habitats for resident and migratory wildlife (Anderson and Ohmart 1980, Hunter et al. 1985). Two major river systems (Colorado and Rio Grande) in the southwestern United States originate within Colorado. While substantial work has been conducted to identify wildlife use and to manage riparian habitats in lower reaches of these river systems (Stevens et al. 1977, Anderson et al. 1978, Anderson and Ohmart 1980, 1985, Swenson and Mullins 1985), little information has been published from studies conducted near the headwaters of these rivers.

The cottonwood-willow (*Populus-Salix*) riparian ecosystem along Colorado's major rivers has the highest wildlife species richness and density in the state (Beidleman 1978, Fitzgerald 1978, Hoover and Wills 1984) and is used by 283 species of vertebrate wildlife. However, most studies have centered on the South Platte River in northeastern Colorado (Graul and Bissell 1978). Wildlife values of riparian habitats along streams and rivers in the mountainous western two-thirds of Colorado have received little study. Among ecosystems in mountainous areas, cottonwood-willow riverbottoms usually possess high values for resident and migratory wildlife (Schrupp 1978, Thomas et al. 1979, Melton et al. 1984). Awareness of these values has increased in recent years along with concern for increasing activities in, and degradation of, these critical wildlife zones (Windell 1980). These habitats are of special concern in mountainous areas because valleys are frequently narrow and centers of human activity.

Before attempting to manage riparian vegetation for wildlife, it is necessary to learn whether these habitats are declining in ability to sustain species richness and abundance. This paper assesses recent changes and status of riparian vegetation along the Rio Grande and Colorado River in southern and western Colorado.

STUDY AREA

Lower-elevation zones of the Rio Grande and Colorado River in Colorado were selected for study (Fig. 1, Table 1). The Colorado River and its tributaries drain about 46,196 km² of western Colorado (Ugland et al. 1984, Vol. 2). The Colorado River is confined to relatively narrow valleys until it is joined by the Gunnison River near Grand Junction where the valley broadens with reduced stream gradient. It leaves the state with flows approximately 75% greater than at the upstream end of the study area (Table 1).

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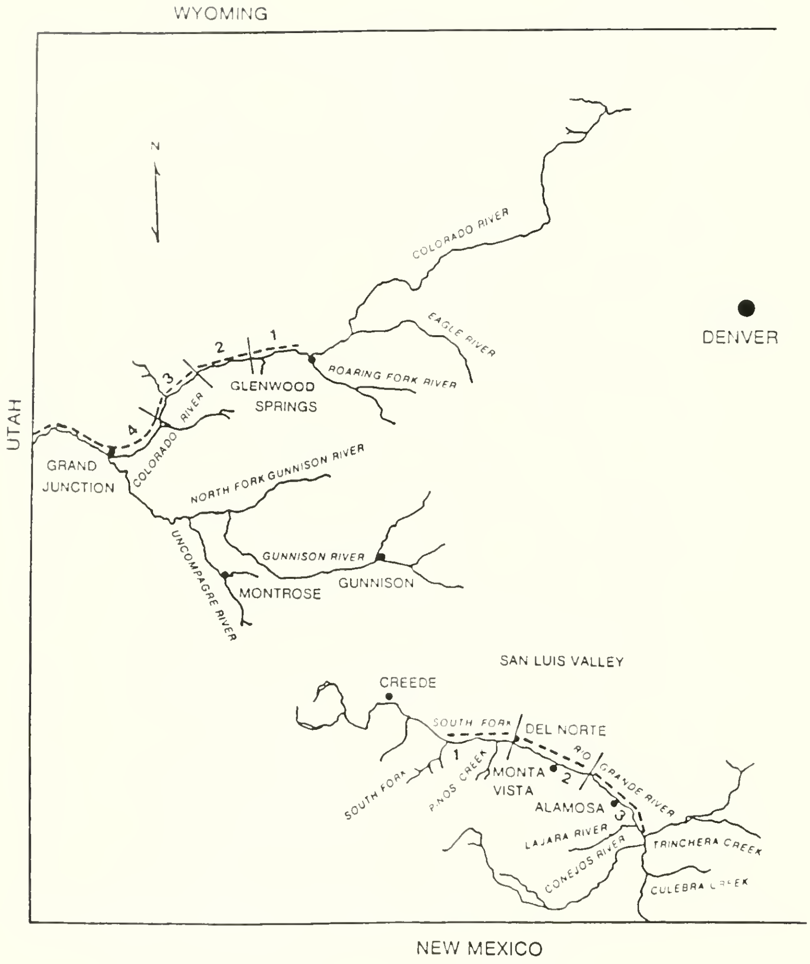
WYOMING
UTAH
NEW MEXICO
N
DENVER
COLORADO RIVER
EAGLE RIVER
ROARING FORK RIVER
GLENWOOD SPRINGS
1
2
3
4
COLORADO RIVER
GRAND JUNCTION
NORTH FORK GUNNISON RIVER
UNCOMPAGRE RIVER
GUNNISON RIVER
GUNNISON
MONTROSE
SAN LUIS VALLEY
CREEDE
SOUTH FORK
DEL NORTE
RIO GRANDE RIVER
SOUTH FORK
PINOS CREEK
MONTA VISTA
ALAMOSA
LAJARA RIVER
CONEJOS RIVER
TRINCHERA CREEK
CULEBRA CREEK

Fig. 1. Colorado River and Rio Grande with inventoried portions (—) and segments (|) in western and south central Colorado.

TABLE 1. Characteristics of variables measured along the Colorado River and Rio Grande, Colorado.

Variable	Colorado River	Rio Grande
$\bar{x}$ sampling interval, yrs[a]	25.0	36.8
Distance sampled, km[b]	167.3	117.4
Sample units	21	20
$\bar{x}$ ha/sample unit	87.0	163.2
Sampling intensity, %	20	27
Elevation, m		
upper	1829	2438
lower	1372	2286
$\bar{x}$ daily stream flow, m^3/s		
upper	100.5	25.3
lower	175.5	7.0

[a] Aerial photos were from 1941 to 1973-83 (Rio Grande) and from 1951-57 to 1980 (Colorado River).

[b] Linear distance was measured at the center of the river channel.

The Rio Grande drains approximately 19,194 km², of which 7612 km² is within a closed basin in south central Colorado (Ugland et al. 1984, Vol. 1). River flow originates primarily in the San Juan Range with lesser amounts from the Sangre de Cristo Range. The river enters the western part of the San Luis Valley, a high-elevation (2286–2438 m) park, and travels through farmed areas for approximately 100 km (where most stream flows are used for irrigation [Table 1]) before entering a canyon that extends into New Mexico.

Harrington (1954) noted that narrowleaf cottonwoods (*P. angustifolia*) dominate along the Rio Grande and upper portions of the Colorado River, whereas lanceleaf cottonwoods

(*P. acuminata*) occur sparsely over a slightly broader elevation range. Rio Grande cottonwoods (*P. wislizeni*) dominate at lower elevations along the Colorado River. Willows are the primary shrubs along the Rio Grande and upper portion of the Colorado River giving way to tamarisk (*Tamarix gallica*) at lower elevations along the latter (plant names follow Harrington [1954]).

METHODS

Approximately 167 km of the Colorado River and 117 km of the Rio Grande were selected for study, and respectively stratified into four and three segments (strata) based on empirical assessments of vegetation (area occupied by cottonwoods, plot width, etc.; Fig. 1). Segments (numbered from upstream to downstream; Fig. 1) were used to distribute random sample units (linear 1.61-km river tracts) more uniformly along the rivers. Twenty sample units were distributed along the Rio Grande, whereas the Colorado River study area contained 21. An electronic planimeter, positioned at mid-channel on U.S. Geological Survey topographic maps, was used to delineate the randomly selected 1.61-km (river mile) sample units. Width of sample units varied and was based on flood plain width, primarily encompassing natural riparian vegetation readily discerned on aerial photos (some adjacent cropland and grassland were included).

The earliest (scale 1:20,000) and most recent (scale 1:40,000) aerial photos available (U.S. Department of Agriculture) were acquired for each sample unit to yield changes over time. The same area was inventoried within each sample unit during both early and recent intervals to assess changes. Earliest aerial photos were from 1941 and the most recent photos were from 1973 through 1983 for the Rio Grande. Those for the Colorado River were from 1951-57 (early) and 1980 (recent).

Interpretative analyses of aerial photos were contracted to the Colorado State Forest Service. Vegetation types, including trees (primarily cottonwoods), shrubs (tamarisk [Colorado River] and willow), hay meadows, grasslands, agriculture (farmland), developed (roads, towns, etc.), river, standing water, and unvegetated (sandbars) were delineated on acetate overlays using a stereoscope. River and unvegetated were combined as river channel. Minor vegetation types (<1% of total area) were omitted. The area per vegetation type was recorded to 0.1 ha using an electronic planimeter. On-site inspections were conducted within several plots along both rivers to verify that photo interpretation was accurately assessing cottonwood stand maturity, canopy cover, and vegetation types. Photo interpretation accuracy approximated 95%.

Maturity classes (trunk diameter) were estimated from tree crown size using photo interpretation. The relationship between trunk diameter and tree crown size was based on previous sampling of cottonwoods along the South Platte River in Morgan County, Colorado (Getter 1977). A close relationship (r^2 = .81) between tree crown size and trunk diameter at breast height (dm dbh) was indicated. However, data relating dbh to tree age were lacking, as increment boring to estimate age of cottonwoods did not yield satisfactory age data. Maturity classes included stands dominated by trees <1.5, 1.5–4.0, 4.1–7.6, and >7.6 dm dbh. Stands of trees were classified by canopy cover as open (10–35%), intermediate (36–55%), and closed (>55%).

Changes in stands of cottonwoods from early to recent photos were analyzed using paired *t* tests appropriate for stratified (segment) samples based on the hypothesis that mean change was zero. Initial tests included analyses of individual maturity/canopy-cover classes; however, sample sizes were inadequate to yield meaningful results. Therefore, maturity-class data for pooled canopy cover classes and canopy-cover data for pooled maturity classes are presented. In addition, early to recent changes were presented, where canopy cover and maturity classes were partitioned. Changes for other cover types were analyzed using paired *t* tests; ANOVA was used to detect differences among segments. Mean comparisons were considered significant at $P \leq .05$.

RESULTS

Colorado River

Estimated loss of cottonwood stands along the Colorado River was 1.9 ha/km sample unit (17.5%; Table 2). Losses in the upper segment (Fig. 1), where cottonwoods initially averaged only 2.2 ha/km, were >90% (Table 3). Area occupied by cottonwoods was highest in segment 2 where they declined 4.4 ha/km. Within downstream segments, cottonwoods averaged

TABLE 2. Area occupied ($\bar{x}$ ha/km) by vegetation/land-use type during early and recent intervals along the Colorado River and Rio Grande, Colorado.

	Colorado River					Rio Grande				
	Early		Recent			Early		Recent		
Type	$\bar{x}$	SE	$\bar{x}$	SE	P	$\bar{x}$	SE	$\bar{x}$	SE	P
Cottonwoods	11.2	2.1	9.2	1.7	NS	17.4	2.9	19.0	3.3	NS
Shrubs	9.5	1.8	10.1	2.1	NS	6.5	0.9	4.9	0.7	<.05
Hay Meadow	14.7	2.9	11.2	3.1	NS	68.6	7.0	54.5	6.3	<.03
Grassland	3.1	0.8	4.1	1.0	NS	0.9	0.6	3.1	1.4	<.05
Agriculture	5.5	1.6	5.1	2.6	NS	0.1	0.1	13.5	5.3	<.03
Developed	0.7	0.3	3.2	0.9	<.01	0.7	0.2	1.0	0.3	NS
River channel	9.3	0.7	8.8	0.8	NS	6.2	0.4	3.9	0.3	<.01
Standing water	0.1	0.05	2.3	0.8	<.03	1.0	0.3	1.2	0.3	NS

TABLE 3. Area occupied/segment ($\bar{x}$ ha/km) by cottonwoods from early to recent sampling intervals along the Colorado River and Rio Grande, Colorado.

	Colorado River					Rio Grande				
	Early		Recent			Early		Recent		
Segment	$\bar{x}$	SE	$\bar{x}$	SE	P	$\bar{x}$	SE	$\bar{x}$	SE	P
Upper	2.3	0.6	0.2	0.1	.02	14.7	1.2	18.4	2.3	NS
Middle	24.0	4.2	19.6	2.3	NS	29.9	3.0	32.2	3.5	NS
Lower	7.8	3.1	7.4	2.2	NS	4.9	2.9	4.3	2.9	NS
Lowest	9.3	1.3	8.2	1.8	NS					

about 7.5–9.3 ha/km and declined at more modest rates.

Fifty-eight percent of the cottonwoods along the Colorado River were in the two younger maturity classes (Fig. 2). The percentage of young trees (dm-dbh) declined almost 50% ($P < .01$) during the 25-year interval. Numbers of large trees (>7.6 dm) also declined dramatically ($P < .02$).

Hectares of cottonwoods were similar among all canopy-cover classes during the early sampling interval. However, by the recent sample interval, open stands increased 11%, whereas intermediate and closed stands declined 42% ($P < .01$) and 27% ($P = .05$), respectively (Fig. 2).

Hay meadow, the most abundant vegetation type along the Colorado River, declined 23.7% during the sample interval (Table 2) with the primary decrease occurring in the lower segment. Grassland occupied 5.7% of the area during early-year sampling but increased 31%. About 10% of the sampled area was in agriculture during both surveys. Developed land and standing water were initially minor but increased to 10% of the total. Overall, river channel changed little, but variance among segments was evident; the channel widened in the two upstream segments and narrowed downstream.

Shrubs, primarily tamarisk, occupied 17–18% of the sampled riverbottom and increased slightly, primarily in the second segment. Shrubs occupied only 1.9–2.5 ha/km within the upper segment, >12.4 ha/km within the second and third segments, and 9.3 ha/km within the lower segment.

Rio Grande

Cottonwoods were moderately abundant within the upper segment of the Rio Grande, increasing 3.7 ha/km (24.9%), and were most abundant within the middle segment where they increased 2.3 ha/km (7.7%; Table 3, Fig. 1). They were absent within several downstream sample units, and estimated loss was 0.7 ha/km (13.8%). Initially, cottonwoods occupied 17.1% of the sampled area, increasing to 18.8% by the second survey (Table 2).

Small trees (<1.5 dm) represented 10.4% of

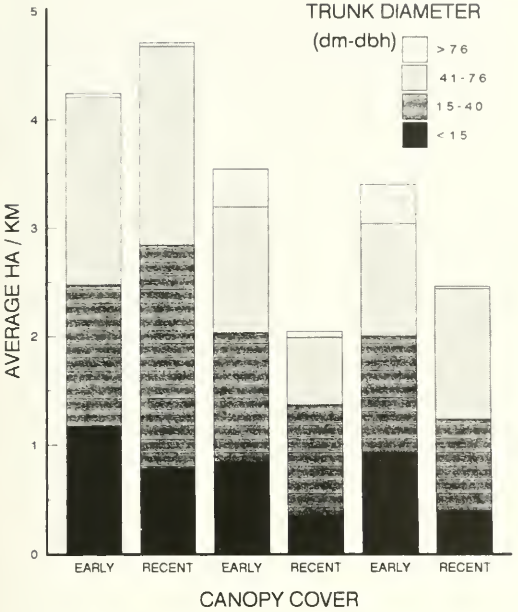

Fig. 2. Early to recent changes/sample in maturity class, and canopy cover of cottonwoods along the lower Colorado River, western Colorado.

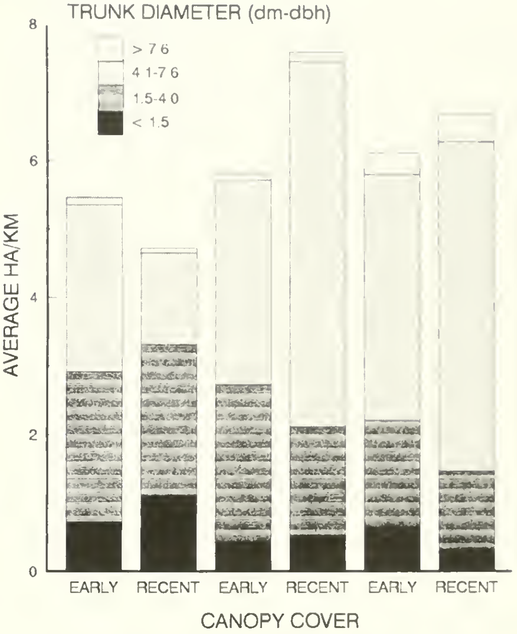

Fig. 3. Early to recent changes/sample in maturity class, and canopy cover of cottonwoods along the lower Rio Grande, southern Colorado.

the composition during both samples and increased 9.3% in occupied area (Fig. 3). Trees of intermediate size (1.5–4.0 dm) declined (P = .13) over the 36.7-year interval, giving way to the next larger (4.1–7.6 dm) maturity class that increased 27.2% (P = .16) (Fig. 3). This latter group dominated among maturity classes during both surveys. Large trees (>7.6 dm) represented only 3% of the total during both surveys and showed little evidence of increasing in occupied area.

Open stands initially occupied 31% of the timbered area and declined (P = .25) to 25% (Fig. 3). In contrast, stands of intermediate closure increased (P = .02) from 33 to 40%. Closed stands increased modestly (P = .49, 9%), representing 35% of the total during both surveys (Fig. 3).

Hay meadows dominated among vegetation types (Table 2), decreasing from 68 to 54% of the sampled area. Declines occurred primarily within the two upper segments. Initially, grassland was minor, but it increased, primarily within the upper segment. Only 2 of 20 samples originally contained cropland, but the proportion increased to 9 of 20 samples (0.1 to 13.4%).

Developed land and standing water were minor components in both early and recent surveys. River channel decreased (36.7%) throughout the study area. Area occupied by shrubs was minor and estimated loss was 25% (Table 2).

DISCUSSION

Comparison of changes along the two rivers leads to greatest concern for habitats along the Colorado River, the much larger of the two (Table 1). The 25-year interval along the Colorado River was considerably less than that for the Rio Grande, but a 17.5% decline occurred in area occupied by trees. Development along the river increased dramatically and replaced many stands of trees.

Lack of natural reproduction and/or high mortality of young trees was indicated by a 50% reduction in stands of young trees along the Colorado River. Reduction of stands dominated by old trees, which provide primary habitat for cavity nesting wildlife, was also evident. However, rapid shifts toward more open stands, which indicated excessive mortality within stands, were more discouraging than changes in maturity structure. Thus, there were fewer and smaller stands and those remaining were more open and occupied by intermediate maturity classes.

Losses of cottonwoods were especially dramatic (>90%) in the upper segment where occurrence was initially low. Expansion of urban areas, highway construction, and other developments were responsible for much of the riparian habitat loss in a relatively narrow valley that initially possessed limited riparian habitat and relatively rapid stream flows. Loss of trees to beaver (*Castor canadensis*) was noted and may be important, especially in the upper segments, since many stands of cottonwoods were confined to streamsides by valley relief.

Expansion of tamarisk was evident along lower reaches of the Colorado River within a broadened floodplain and slower stream flows. Increasing expansion of tamarisk severely limits opportunities for natural regeneration of cottonwoods and willows. Russian olive (*Elaeagnus angustifolia*) also is pioneering along the Colorado River. This species possesses a growth form of intermediate height and, like tamarisk, may form monocultures (Knopf and Olson 1984).

Stream flows along the Colorado River have not shown major declines in recent decades. Large impoundments and high-elevation diversions, primarily occurring during the last 50 years, have altered and reduced peak flow sequences on the Colorado and Gunnison rivers.

Extensive flooding occurred along the Colorado River in 1983-84, resulting in considerable natural reproduction of seedlings. However, infrequent flooding is not likely to offset the impacts of stream flow regulation, streamside developments, and invasions of exotic species. Vegetation conditions and changes along the Colorado River appear to be following the pattern of disrupted recruitment of native riparian phreatophytes occurring along many western rivers (Howe and Knopf 1991).

In contrast to changes documented along the Colorado River, riparian habitats along the Rio Grande were relatively stable during the sample interval, with an increase in area occupied by cottonwoods. However, several of the sample units within the lower segment contained few or no cottonwoods. Little evidence of seedling establishment was noted subsequent to increased stream flows during 1983-84, which raises concern for future trends. Stream flows averaged over 10-year intervals since 1890 showed little evidence of decline at Del Norte in the west central portion of the San Luis Valley (Ugland et al. 1984, Vol. 1). However, upstream impoundments have reduced peak flows and altered patterns with stabilized increased volumes into late summer for irrigation. Flows downstream at Alamosa (Fig. 1) averaged about 30% of those at Del Norte, and average flows since 1930 have been about one-half of those from 1913 to 1930. Reduction in channel width was indicative of reduced and stabilized stream flows. Streamsides were dominated by perennial herbaceous vegetation, which provides limited opportunity for establishment of pioneering species such as cottonwoods and is indicative of moderately stable and slow stream flows through the relatively flat San Luis Valley. Increased farmland was the most pronounced land-use change along the Rio Grande, whereas little development occurred.

Shrubs (primarily willows) have not been major components along the Rio Grande in recent decades. Severe cold winters, due to high elevations (Table 1), may prevent invasions of tamarisk, which has developed as a streamside monoculture at lower elevations elsewhere along riparian systems in the Southwest. Russian olive was not yet invading the inventoried Rio Grande riverbottom.

Similar inventories of riparian vegetation changes and status were conducted along the South Platte and Arkansas rivers in the High Plains of eastern Colorado (Snyder and Miller 1991). Deterioration of habitat along the Arkansas River was much greater than along western rivers in Colorado. However, conditions along the Colorado River seemed to be deteriorating more rapidly than along the South Platte River. There was also much less riparian habitat along western rivers, making that which remained of greater importance. Sampling of changes between two points in time may not give an accurate assessment of long-term trends. A third inventory of these same sample units is recommended in the near future.

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RESIDENT UTAH DEER HUNTERS' PREFERENCES FOR MANAGEMENT OPTIONS

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ABSTRACT.—A total of 3291 resident deer hunters returned questionnaires distributed at checking stations in fall 1989 and 1990 providing opinions and management data concerning the Utah rifle hunt. Hunters reported hunter crowding and too few big bucks as critical reasons for possibly choosing to quit deer hunting in Utah. Indeed, hunter age structure and measured satisfaction suggested a negative future trend in hunter participation. Results suggested the adoption of several hunter-preferred management options would increase satisfaction, motivation, and success.

Key words: mule deer, questionnaires, checking stations, deer management, hunter opinions, wildlife methods, wildlife techniques.

Competition for wildlife recreation in the Rocky Mountain region will increase in the future, while projected populations of major wildlife species will show little change. In the next 30 years the number of big game hunters is expected to slowly increase from about 1.5 to 1.7 million, compared with the rapid increase in nonconsumptive users of 3.9 to 7.1 million (Flather and Hoekstra 1989). Certainly, the percentage of hunters in the total population will decline, while the percentage of nonconsumptive users will increase. Consequently, to balance resource use, wildlife managers must obtain a clear understanding of user preferences, particularly among those users who historically and currently have paid most management costs via license permit fees and excise taxes on sporting equipment.

In Utah, mule deer are preeminent among hunted wildlife species in terms of income received for wildlife management and hunter days afield. However, compared with the 1970s and in contrast to past regional trends (Flather and Hoekstra 1989), total big game license sales decreased slightly (0.8%) in the 1980s while total rifle hunters afield declined 3.1% (Jense and Shields 1990). These figures warn of possible negative trends for deer hunter participation and, along with uncertain hunter satisfaction, strongly suggest a need for constant and effective communication between state wildlife officials and Utah hunters.

One means of communicating information is through hunter opinion questionnaires, which have become an important data source for game management decisions. In Utah during the 1980s, six questionnaire surveys were conducted, and that number will likely double in the 1990s (Bunnell and Austin 1990). The use of postcard questionnaire surveys distributed to homeward bound hunters at deer checking stations is one method. This simple technique, developed in Utah during the late 1980s, is inexpensive, demographically unbiased, and accurately representative of hunters' opinions concerning deer management (Austin and Jordan 1989, Austin et al. 1990).

METHODS

Questionnaires[3] were printed on 4 1/4 × 6-inch postage-paid cards. During opening weekend of the 1989 Utah rifle deer hunt, 7040 questionnaires were distributed to hunters at 11 checking stations, and in 1990, 8750 questionnaires were distributed at 16 locations. One questionnaire was given to each licensed hunter checked until the supply was exhausted.

Data were analyzed within years using the Pearson chi-square statistic. The cross-tabulation method from the SPSS program on a VAX

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TABLE 1. Questionnaire return rates.

		1989 Survey			1990 Survey		
Region	Location	No. distributed	No. returned	% returned	No. distributed	No. returned	% returned
Northern	Snowville	500	107	21.4	500	109	21.8
	Blacksmith	500	95	19.0	500	83	16.6
	Ogden	1000	151	15.1	500	126	25.2
	Kamas	—	—	—	500	91	18.2
	Wellsville	72	20	27.8	—	—	—
Salt Lake	Canyons	—	—	—	250	48	19.2
Northeastern	Vernal	666	44	6.6	500	114	22.8
	Bookcliffs	650	131	20.2	500	113	22.6
	Current Ck.	—	—	—	500	120	24.0
Central	Thistle	1000	206	20.6	1250	291	23.3
	Tucker	300	37	12.3	—	—	—
	Sheepcreek	300	48	16.0	250	41	16.4
	Vernon	452	151	33.4	375	95	25.3
	Stansbury	—	—	—	300	57	19.0
Southeastern	Areawide	—	—	—	830	95	11.4
South central	Fishlake	—	—	—	300	14	4.7
	Oak Creek	—	—	—	195	63	32.3
Southern	Bloomington	1600	423	26.4	1500	418	27.9
Total		7040	1413	20.1	8750	1878	21.5

computer was used. For question number 18, 1990 survey, the values given were objectively placed into 11 monetary classes for analysis. The significance level for all data interactions was set at $P < .05$. For question number 20, 1990 survey, because the question was written with innumerable potential responses and many questionnaires contained more than one response, data were not statistically analyzed but are reported numerically. The responses were subjectively grouped into 71 categories. Data from the 1987 and 1988 surveys are added and compared where applicable.

RESULTS

Return Rates

Checking stations used for distribution by Utah Division of Wildlife Resources regions, the number of questionnaires distributed, and return rates are shown in Table 1. Although rates varied considerably by region and location, total return rates were 20.1% in 1989 and 21.5% in 1990, and consistent (Austin and Jordan 1989, Austin et al. 1990) with those reported for 1987 (25.8%) and 1988 (20.1%). Expected statewide return rates using this method are thus about 20–25%.

Hunter Demographics, Success, and Satisfaction

Most resident hunters are male (>90%), age 25–44 (52%), and have more than 10 years of Utah deer hunting experience (>60%). During 1989 and 1990, hunters had less than 50% party success for bucks on opening weekend and relatively low hunter satisfaction (Table 2). Hunter party success noticeably declined between 1987 and 1988 and again between 1988 and 1989, but remained about the same between 1989 and 1990.

The percentage of hunters (<20%) in the youngest age class (14–24 years) is lower than expected. Participation by hunters in this age class should be highest because few people begin hunting after about age 25. These figures, consistent over four years, alone suggest possible future declines in the number of Utah deer hunters. However, the sharp drop in hunter participation between the third and fourth age

TABLE 2. Demographics, party success (%), and hunter satisfaction of Utah resident deer hunters sampled, 1987–1990 (sample sizes in parentheses).

	Sex			Age class[a]						
Year	Male	Female	N	1	2	3	4	5	6	N
1987	90.4	9.6	(863)	19.0[e]	31.8	23.0	14.2	8.1	4.0	(869)
1988	89.6	10.4	(444)	19.7	33.0	23.4	13.8	8.3	2.0	(458)
1989	92.8	7.2	(925)	18.6	28.1	25.9	13.9	9.0	4.6	(936)
1990	92.7	7.3	(1429)	22.0	26.6	26.2	12.9	8.2	4.1	(1429)
Means	91.4	8.6		19.8	29.9	24.6	13.7	8.4	3.7	

	Experience class[b]								
Year	1	2	3	4	N	Success[c]		Satisfaction[d]	
1987	18.7	21.3	27.2	32.8	(867)	69.3[f]	(411)	5.3	(871)
1988	21.7	18.4	28.4	31.5	(461)	55.3	(459)	4.3	(456)
1989	22.7	15.2	25.2	36.8	(932)	48.0	(904)	4.1	(934)
1990	25.1	14.2	26.0	34.6	(1418)	47.9	(1406)	4.6	(1413)
Means	22.1	17.3	26.7	33.9		55.1		4.6	

[a] Age classes: 1 = 14–24, 2 = 25–34, 3 = 35–44, 4 = 45–54, 5 = 55–64, 6 = 65+ years

[b] Experience classes: 1 = 1–5, 2 = 6–10, 3 = 11–20, 4 = 21+ years

[c] Hunting party success for one or more bucks on opening weekend

[d] Hunter satisfaction of current year's hunt in comparison to all previous deer hunts. A score of 5.0 would be expected for the average hunt

[e] Age class 16–24. Hunters aged 14 and 15 years were ineligible for big game licenses

[f] Hunting party success for bucks and antlerless deer on this hunt. For the 1987 season 62,516 bucks and 1168 antlerless deer were harvested.

classes (35–44 and 45–54) is also of concern because in these age groups many hunters' children are beginning to hunt, and parent participation is a key factor in long-term sustained interest of new hunters (Decker and Connelly 1989). Mean age of all hunters was 36.3, 35.4, 37.0, and 36.0 years for 1987–90, respectively. In a completely randomized survey of Utah hunters, Krannich et al. (1991) reported a mean age of 37 years and similar hunter age and sex characteristics.

One probable explanation for the sharp drop in hunters in the 45–54 age class is the significant interaction between age and hunter experience with hunter satisfaction ($P < .04$). Hunters with 20+ years of experience, who generally hunted deer before the 1970s when the number of hunters was lower (Fig. 1) and hunter success rate was higher (Jense and Shields 1990), show lower satisfaction scores than younger, less-experienced hunters. Mean satisfaction scores of experience classes 1–3 versus 4 (Table 2) for both years combined were 4.5 and 3.9, respectively. Similarly, mean satisfaction scores of age classes 1–3 versus 4 were 4.5 and 3.7, respectively. Consequently, hunting motivation for hunters with 20+ years of experience has likely decreased because of perceived lower-quality hunting.

Another concern for hunter participation is noted by comparing the trend of hunter participation by experience classes between survey years (Table 2). No trends in hunter participation were evident for hunters with 11 or more years of experience. However, hunters with 6–10 years of experience decreased 7.1% between 1987 and 1990, while hunters with 1–5 years of experience increased 6.4%.

Comparison Between Hunt Types

Utah has had four basic types of hunts since 1951, with each hunt type having a variable number of antlerless control permits. Either-sex hunts dominated from 1951 to 1973, with buck-only hunts dominating from 1974 to 1990, as well as before 1951. From 1985 to 1990 hunter-number-restrictive (limited-entry and high-country) hunts, and from 1984 to 1989 antler-restrictive (three-point-and-better) hunts were established on some units.

BUCK-ONLY HUNTS.—Total buck harvest averaged 63,250 per year with 8633 antlerless harvest and 181,235 hunters afield (Fig. 1). The number of unretrieved deer reported per 100 buck-only hunters in these surveys for 1987–90 was 19.9, 21.7, 15.9, and 16.0, respectively. Using the weighted mean of 17.9, total unretrieved deer for this period was 32,441 per

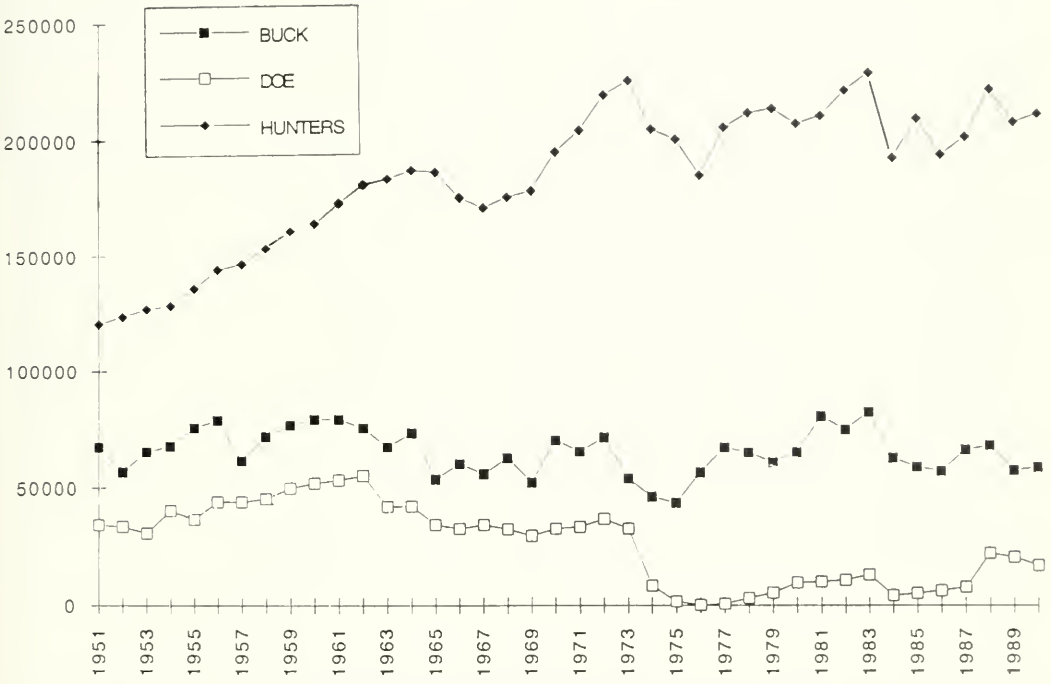

Fig. 1. Total harvest of buck and antlerless deer and combined hunters afield from all buck hunts in Utah, 1951–90.

year, and mean total annual hunting mortality was 104,324. Mean hunter satisfaction (1987–90), with 0 representing the worst hunt and 10 the best hunt, was 4.4. Hunting party success was 45.8%.

EITHER-SEX HUNTS.—During 23 years of either-sex hunting, the statewide total buck harvest averaged 66,992, and the antlerless harvest was 39,228. Using the estimated mean for unretrieved deer (Robinette et al. 1977, Stapley 1970) of 8.0 deer per 100 hunters and the mean number of rifle hunters afield (153,666), a calculated yearly loss of 12,293 unretrieved deer is obtained, bringing the mean total annual hunting mortality to 118,513. Hunter preference for buck-only versus either-sex hunting has not been addressed.

ANTLER-RESTRICTIVE HUNTS.— Three-point-and-better, antler-restrictive hunts were available on some units during 1984–89, and then discontinued. In comparison with buck-only hunts, three-point-and-better hunts showed a reduction in hunters afield, buck harvest, and hunter success (Jense 1990). However, these hunts also showed a small increase in the post-season total buck to doe ratios, but a large decrease in the number of post-season, mature bucks counted. These areas also showed a large decrease in the small buck (two-point-and-less) to doe ratio between preseason and post-season classification counts (Jense 1990).

Our analysis confirmed the adverse impacts of three-point-and-better hunts reported by Jense (1990), with the highest number of unretrieved deer at 39.6 per 100 hunters, including 21.7 bucks. This number of bucks, mostly two-point-and-less, is compared to 4.6 bucks per 100 hunters on buck-only areas. However, hunters from antler-restrictive areas were moderately satisfied, with a mean index of 4.8, and mean hunting party success was 55.6%. During 1989, the last year of three-point-and-better hunts, 40.0% (*n* = 931) of Utah resident hunters had hunted at least once on three-point-and-better areas, but only 26.7% (*n* = 906) preferred to continue this type of hunt. Indeed, less than half (47.7%) of hunters who chose to hunt these units in 1989 preferred to continue them.

Even though antler-restrictive hunts were not successful over entire deer management units, selection of conscientious hunters to avoid high unretrieved deer losses may lead to successful antler-restrictive management. For example, at the East Canyon Resort (10,000 acres) in northern Utah, protecting only 2 × 2 point bucks (1988–90) increased the mean number of total antler tines of harvested bucks from 4.5 (1985–87) to 6.1 (1988–90). The percent of harvested bucks 2 × 2 or smaller decreased from 60 to 35%, while the number of trophy bucks larger than 4 × 4 increased from 0 to 8 (unpublished data, East Canyon Resort).

HUNTER-NUMBER-RESTRICTION HUNTS.—Limited-entry hunts have been used on some units since 1985. In comparison with buck-only hunts, they provide higher hunter success ($P < .01$) and satisfaction ($P < .001$), with an index of 6.3, but no difference in the total number of unretrieved deer (17.7 total deer per 100 hunters with 9.1 bucks and 8.6 antlerless). Hunting party success (1987–90) was high at 68.8%. In 1989, 22.8% of resident hunters (n = 935) had hunted deer on limited-entry areas, and most (65.6%) indicated the fee of $22.00 was fair. While most hunters (n = 908) favored the same (37.8%) or increased (38.9%) number of limited-entry units, hunter preferences for various permit drawing and landowner hunting options were unclear.

A second type of hunter-number-restrictive hunt is the high-country hunt. This uncrowded, high-quality hunt—but one that harvests bucks not then available during the October rifle hunt—received positive support from most (59.6%) Utah hunters.

Vehicle Access to Public Lands

A strong majority of hunters (76.2%) indicated that at least some lands should be closed to vehicle access during the deer hunt to increase the quality of the hunting experience. However, the percentage of hunters indicating at least half of all public lands should be open to vehicles was 74.5%. Overall, hunters indicated that a mean of 37.5% of public lands should be closed to vehicle access, varying by location from 28.9 to 45.4% The percentage of hunters who hunted on areas with vehicle restrictions was 33.8%, while the percentage of hunters who indicated preference to hunt on areas with vehicle restrictions was 45.2%. Using the logical assumption that the percentage of areas restricted to vehicles should be closely proportional to the percentage of hunters preferring them, our data suggest the current amount of area with restricted vehicle access is close to hunter preference, but that an additional 3.7% (37.5–33.8) to 11.4% (45.2–33.8) of public lands should be restricted. More information is needed on hunter preferences for vehicle-restricted areas in terms of size, locations, and number of areas.

License Fees

With the current cost of a big game hunting license set at $15.00, hunters were asked what they believed to be the fair value. Although Schreyer et al. (1989) reported increased license fees were opposed by most hunters, a mean value of $15.90 was determined ($n$ = 1391) in our study. Most hunters (58.8%) indicated $15.00 was the fair value. Sixty-eight hunters (4.9%) indicated the fair value was $30.00 or more, while 58 hunters (4.1%) indicated the value was less than $10.00. It was interesting to note that costs were not related to hunter success, satisfaction, hunter choice of hunt type, or whether private or public lands were hunted.

Although license fees are strongly and broadly approved by Utah hunters, few improvements in the quality of the deer hunt can be made without the economic trade-off of increased hunter fees. Hunter preferences for balancing potential increased fees with increased hunt quality need to be defined.

Hunter Concerns

Twenty-five categorical responses were given by 1% or more hunters as reason to quit deer hunting (Table 3). Although the list contains several areas of low management influence, such as old age, high associated costs of hunting, and personal attitude, most areas of responses are influenced by management decisions. The most common reasons, directly influenced by management decisions, included too many hunters, too few deer, bucks, and big bucks, private land problems, and poor game management.

DISCUSSION

Reasons to Quit Deer Hunting

The proportion of mature bucks in the harvest is an area of management control. It is clear most hunters prefer harvesting large bucks infrequently as opposed to harvesting smaller bucks frequently (Austin et al. 1990), as well as reducing some hunting opportunity to increase the proportion of mature bucks in the harvest (Austin and Jordan 1989, Toweill and Allen 1990). Furthermore, with the hunting media emphasis on trophy bucks, the potential harvest of mature bucks adds considerably to hunter

TABLE 3. Utah resident deer hunters' responses to the question: If you were to quit deer hunting in Utah, what reason would you list?

Number of questionnaires returned:	1430
Number of questionnaires with no response:	88
Number of questionnaires with "would not quit, none":	46
Number of questionnaires with responses:	1296
Number of total responses:	2087

Response categories	Number of responses	% hunters
Too many hunters	479	37.0
Too few deer	199	15.4
Private land problems	164	12.7
Too few big bucks	122	9.4
Old age or physical impairment	108	8.3
High associated costs of hunting	83	6.4
No areas to hunt or access to public lands	81	6.3
Too few bucks	79	6.1
Poor game management	75	5.8
Unethical hunters	72	5.6
Low success or no limit on statewide license sales	63	4.9
Children aged 14 and 15 years can hunt	48	3.7
Deer are too small	44	3.4
Too much ATV use or too many road hunters	41	3.2
Safety	39	3.0
High costs of licenses	35	2.7
Personal attitude	33	2.5
Too few vehicle access roads	31	2.4
Too many nonresident hunters	30	2.3
Poor hunt quality	29	2.2
Proclamation too long or complicated	27	2.1
No either-sex or antler-restriction hunts	19	1.5
Too many limited-entry areas	17	1.3
Too few limited-entry areas	16	1.2
Too many does	14	1.1
46 other categories	139	10.7

motivation, and Kramich et al. (1991) reported that about two-thirds of hunters (66.3%) were dissatisfied with the size of bucks.

Compared with either-sex hunting, age structure of the male population declines under buck-only hunting (McCullough 1979). In Utah (Austin 1991), the percentage of mature bucks, age 3 1/2 years and older, harvested decreased from about 44% during the pre-1951 buck-only hunts to about 30% during the period of either-sex hunting (1951–73). The percentage of mature bucks harvested sharply decreased and has remained at about 10% during the period of reestablished buck-only hunting (1974–90). On limited-entry hunts, the percentage of mature bucks in the harvest has exceeded 30% on most units. Not only has size of harvested bucks decreased due to decreasing mean age, but age-specific size has also declined (Austin et al. 1989).

The authors believe a reasonably high percentage (20–40%) of mature bucks in the harvest is critical to successful deer management and hunter motivation. It is clear to us that decreased hunting pressure on the buck population is necessary. The data strongly suggest a need to establish statewide minimum standards for (1) age structure of the buck harvest, (2) post-season buck:doe ratios, and (3) hunter success for bucks.

Problems associated with private lands are important to hunters. These problems include poorly marked lands, trespass, private lands curtailing access to public lands, and depredation. Private lands provide deer hunting for 14.8% (1990 survey) of Utah resident hunters, and 14.7% of hunters reported owning 10 or more acres used by wildlife (1989 survey). One possible, partial solution may be to give landowners more flexibility in management by allowing either-sex hunting on private lands. Advantages include increased landowner control over deer numbers on their lands, decreased unretrieved deer kill (Austin et al. 1990), reduced depredation complaints, and improved opportunity for harvest. Furthermore, liberal hunts on private lands may increase incentives for landowners to mark their boundaries and allow additional hunting opportunity.

The categories of unethical hunters, safety, and minimum age for hunters are closely related to hunter education courses. Since the beginning of the hunter education program (1958) and the required wearing of hunter-orange clothing (1973), the mean number of total Utah hunting accidents and fatalities per year has averaged 11.1 and 3.4, respectively, with about three accidents and one fatality occurring during the rifle hunt. Before about 1958 when neither hunter education nor hunter orange was required, over 100 accidents and about 20 fatalities occurred yearly from all hunts combined. Hunter preference to allow persons aged 14 and 15 years to hunt big game has not been addressed.

The length and complexity of the proclamation is a concern of hunters. Before 1979, the one-page Utah deer proclamation measured 17.5 × 22.5 inches and was printed on high-quality paper, with the rules and regulations on one side and a multicolored map of Utah's deer units on the reverse. In 1990, the newsprint proclamation sheets were close to the same size (14.5 × 23.0 inches), but contained six pages.

The quality of the hunt in terms of the ratio of deer or bucks harvested per hunter is controlled by management. Although management can alter the buck:doe ratio, the total number of deer is limited by habitat, and, conversely, hunters have not been numerically limited. The Utah buck harvest has remained rather constant, mostly 50,000–80,000, since 1951 (Fig. 1), while the antlerless harvest has sharply decreased since 1974 with the resumption of buck-only hunting. Total buck hunters afield from all combined hunts increased steadily between 1951 and 1964, decreased for three years (1964–67), slowly increased during 1967–69, but abruptly increased between 1969 and 1973. After a second three-year period of decreasing hunters afield (1973–76), hunter numbers have fluctuated but remained high throughout the 1970s and 1980s. Consequently, the hunter responses of poor game management, poor hunt quality, the lack of either-sex hunts, and too many does, especially since changes to buck-only management were made beginning in 1974, have merit.

Hunter crowding before about 1969 when license sales were less than 180,000 (Fig. 1) was probably a much smaller problem (Bureau of Government and Opinion Research 1971). However, the crowding problem of increased human population and finite resources (Leopold 1930) has been exacerbated because of the long-term (Leopold 1919) and more recent increasing urbanization, closures of private lands to public hunting, and increased vehicle access on both private and public lands (Mann 1977, Reed 1981).

Our findings indicate the majority of hunters prefer reduced hunting opportunity for higher quality. When hunters were asked to indicate the effect of crowding on their hunt quality, using an 11-point scale where 0 means crowding greatly decreased the quality and 10 means crowding had no negative effect, only 27.8% of hunters (scale: 8,9,10) indicated crowding had little effect compared to 60.2% of hunters (scale: 0–5) who indicated a large effect ($\bar{x}$ = 4.92). Krannich et al. (1991) reported 71% of hunters believed there were too many hunters in their areas. Crowding effects were not significantly related to hunter age, sex, years of experience, unretrieved deer reported, or whether hunters were on private or public lands. Surprisingly, the means for hunters from successful (5.04) and unsuccessful parties (4.96) were not different. These data indicate the effects of crowding are felt by almost all groups equally. However, hunters from limited-entry areas ($P < .002$), where hunter numbers are limited, rated the effect of crowding less negatively ($\bar{x}$ = 6.16), while hunters preferring to hunt in areas restricted from vehicles were more ($P < .001$) negatively affected ($\bar{x}$ = 4.61) than hunters preferring no restrictions ($\bar{x}$ = 5.50).

Management Options to Reduce Hunter Crowding

Several options are available to reduce hunter crowding. Split deer hunting seasons were opposed by Utah hunters in recent studies (Krannich and Cundy 1989, Austin et al. 1990, Krannich et al. 1991). This option would likely increase hunting pressure on bucks by increased hunter days, longer seasons, and hunting during the more vulnerable rutting period; it would thereby further decrease mean age and size of harvested bucks.

A second option is to require hunters to choose either a buck or doe tag. Our survey indicated 78.4% of resident hunters would choose a buck tag, which would reduce buck hunting pressure by about 21.6%.

A third option is to require hunters to choose and hunt only one season. Since mean hunters afield for 1988–89 combined were archery = 26,613, rifle = 180,298, and muzzleloader = 8832, this option would reduce crowding during the rifle hunt up to approximately 20% assuming hunter proportions remained about the same. Hunters favor this option: in our 1989 and 1990 surveys, 63.8 and 64.0%, respectively. In a 1990 completely randomized telephone survey of 14,305 deer hunters, 58.0% of Utah hunters indicated preference for this option. Krannich et al. (1991) reported a similar level of support (mean score = 6.19) using a scale of 0–10.

Probably the most effective option to permanently reduce hunter crowding, while at the same time establishing a minimum standard for quality in terms of hunter pressure on bucks, is to limit license sales of buck tags. Hunters consistently favor this option. In our 1990 survey, 60.6% of resident hunters preferred to limit buck license sales to 150,000, with up to 35,000 antlerless tags available to unsuccessful buck tag applicants; 39.4% favored unlimited license sales. Since hunters who favored limiting license sales also favored having to choose sex of tag ($P < .004$), most hunters would favor having to choose sex of tag. Krannich et al. (1991) determined most hunters (61.7%) supported choosing the sex of tag and having yearly harvest restricted to one deer per hunter.

In the 1989 survey, only 36.6% of hunters indicated preference to hunt every year regardless of future growth in hunter numbers, while the majority (63.4%) selected some level of hunter number limitation (Austin et al. 1990). Of hunters preferring the limitation, 38.2% selected the limit at 160,000 and 25.2% selected the 200,000 limit. Previously in 1987, 55.8% of hunters showed preference to limit hunters to less than 200,000 (Austin and Jordan 1989).

It is apparent to the authors that some restrictions are needed. We believe the increased buck hunting pressure beginning in 1970 (Fig. 1) has had negative effects on hunter success, satisfaction, motivation, and harvested-buck size. These negative effects appear to outweigh the values of increased wildlife management income and hunting recreation opportunity. Indeed, hunter responses from these surveys confirm our view that hunting pressure on bucks should be reduced to the pre-1970 level.

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LIST OF OREGON SCOLYTIDAE (COLEOPTERA) AND NOTES ON NEW RECORDS

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ABSTRACT.—Listed are 121 species of Scolytidae from Oregon. Ten species are reported from Oregon for the first time *Hylastes tenuis* Eichhoff, *Phloeosinus scopulorum scopulorum* Swaine, *Phloeosinus hoferi* Blackman, *Trypodendron betulae* Swaine, *Xyleborus xylographus* (Say), *Trypophloeus striatulus* (Mannerheim), *T. thatcheri* Wood, *Procryphalus mucronatus* (LeConte), *Pityophthorus scalptor* Blackman, and *Monarthrum dentigerum* (LeConte). The second Oregon specimen of an exotic species, *Xyleborus californicus* Wood, is reported also.

Key words: Scolytidae, faunal list, Oregon.

Oregon is a large state with diverse vegetation that occurs there due largely to the wide range of physical and climatic environments. The climate results in part from the interplay between maritime and continental air masses and the intervening Cascade Mountain Range that divides the state into distinct western (maritime) and eastern (continental) regions (Franklin and Dyrness 1973). For example, average annual precipitation varies from approximately 60–300 cm west of the Cascades to 20–100 cm eastward.

The exceptionally diverse forests of southwestern Oregon have an affinity with California, whereas those of northeastern Oregon are related to Rocky Mountain forest types. Because Scolytidae are host-specific to some degree, their distribution in Oregon is linked closely to the distribution of species of trees and shrubs.

Oregon scolytids were listed by Chamberlin (1917), but that list is greatly out of date. We herein update the list to include records and synonymies published by Wood (1982). Similar lists have been published recently for Idaho (Furniss and Johnson 1987) and Montana (Gast et al. 1989).

Six species not previously reported from Oregon were collected by us on field trips in 1990, and four species were found among museum specimens. More species will surely be found by further collecting. They likely will include more *Pityophthorus*, a genus that is relatively rich in species in western forests and elsewhere; and species of other genera from the diverse California fauna (Bright and Stark 1973) that infest trees endemic to both states.

Other new scolytids are likely to be introduced accidentally by commerce. For example, the exotic *Xyleborus affinis* Eichhoff was intercepted in 1961 at Portland in *Dracaena massangeana* from Puerto Rico. Of the 121 species listed here, 8 are clearly exotics that have become established at unknown times: *Hylastinus obscurus* (Marsham), *Scolytus rugulosus* (Müller), *S. multistriatus* (Marsham), *Xyleborus dispar* (Fabricius), *X. xylographus* (Say), *X. californicus* Wood, *Xyleborinus saxeseni* (Ratzeburg), and *Monarthrum dentigerum* (LeConte). Of these, *X. californicus* was known heretofore in Oregon from only one specimen (Wood 1982); a second specimen was caught (by JBJ) in flight after sunset, 6-VIII-1990, Champoeg State Park, Marion Co. It probably was introduced by commerce at Portland, although its native range is still unknown. We speculate that it may infest distressed deciduous trees along the Willamette River.

By their habits, Oregon Scolytidae are characterized as true bark beetles, living in cambium (105 species); ambrosia beetles, living in xylem although they may feed entirely or partly on fungi that they transmit (14 species), living in pine cones (*Conophthorus ponderosae* Hopkins), or living in roots of clover (*H. obscurus*). Conifers are hosts of 98 species, while the other 23 species occur in angiosperms.

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Abbreviations of repositories listed for specimens new to Oregon are: ODAC = Oregon Department of Agriculture collection, Salem; PNW = Pacific Northwest Forest and Range Experiment Station collection, Forest Service, USDA, Corvallis, Oregon; WFBM = W. F. Barr Entomological Museum, University of Idaho, Moscow, Idaho; and SLW = Stephen L. Wood collection, Brigham Young University, Provo, Utah.

SPECIES NEW TO OREGON

Subfamily Hylesininae

Hylastes tenuis Eichhoff

BIOLOGY.—Monogynous. Infests *Pinus* spp., presumably the roots.

DISTRIBUTION AND NOTES.—MEXICO: Hildago and Mexico (state); USA: Mass. to Fla., all southern states westward to Calif., and Ida. OREGON: Eugene, Lane Co., 22-IX-1971, black light trap, K. J. Goeden (1 ODAC). Prineville, Crook Co., 25-VII-1934 (1 PNW), VIII-1935 (1 PNW), *Pinus ponderosa*, Hopk. 18960-83, W. J. Buckhorn (paratypes of the synonym, *H. minutus* Blackman).

Phloeosinus scopulorum scopulorum Swaine

BIOLOGY.—Monogynous. Infests stems of *Juniperus scopulorum*. Galleries parallel to grain with a nuptial chamber just above the entrance, appearing as though the chamber were halved and one side shifted forward half its diameter (Bright 1976, Fig. 182).

DISTRIBUTION AND NOTES.—CANADA: Alta., B.C.; USA: Wash. OREGON: Sisters, Deschutes Co., 8-V-1978, *Juniperus* sp., R. L. Penrose (4 ♀, 3 ♂ ODAC). Canby, Klackamas Co., April 15, 1965, K. J. Goeden (1 ♂ ODA). North Plains, Washington Co., 20-IV-1969, *Thuja plicata*, K. J. Goeden (2 ♂, 1 ♀ ODA, 2 ♂ SLW). Portland, Multnomah Co., 22-X-1971, *Chamaecyparis lawsoniana*, R. L. Westcott (1 ♀, 1 ♂ ODA, 1 ♀ SLW). Northbend, Coos Co., 9-VI-1974, on cypress, J. McLaughlin. (3 ♀ ODA).

Phloeosinus hoferi Blackman

BIOLOGY.—Monogynous. Infests branches of *Juniperus deppeana*, *J. osteosperma*, and *J. scopulorum*.

DISTRIBUTION AND NOTES.—CANADA: B.C.; USA: all western states except Wash. OREGON: about 9 km W Enterprise, Wallowa Co., 9-XI-1990, *Juniperus scopulorum*, M. M. Furniss and A. Equihua (12 ♀, 5 ♂ WFBM). Infesting branches, 0.5–3.0-cm diameter, of a small standing tree. Larvae parasitized by an abundant braconid wasp, *Ecphylus* sp., probably *californicus* Rohwer. Host is restricted in Oregon to the vicinity of the Wallowa River, for a distance of approximately 30 km downstream from Enterprise.

Subfamily Scolytinae

Trypodendron betulae Swaine

BIOLOGY.—Monogynous. Infests *Betula* spp., rare in *Alnus* spp. Tunnels are constructed by females radially into sapwood. Other females construct branches from the radially aligned tunnel at close intervals, left or right, in the horizontal plane. Eggs are laid in niches oriented above and below the gallery. Larvae excavate short cradles in which they develop and feed on ambrosia fungus. Males are active in keeping the tunnels clean and aerated.

DISTRIBUTION AND NOTES.—CANADA: Alta., B.C., Man., N.B., N.S., N.W.T., Ont., Que.; USA: Ida., Me., Mass., Minn., Mont., N.H., N.J., N.Y., S.D., Wisc. OREGON: Mill Creek, Umatilla Co., 8-XI-1990, *Betula papyrifera*, M. M. Furniss and A. Equihua (1 ♀, 3 ♂ WFBM, 1 ♀, 1 ♂ ODAC). Infesting lower stem of a 23-cm-diameter wind-felled tree. Also present were *Xyleborus dispar* (Fabricius) and *Xyleborinus saxeseni* (Ratzeburg).

Xyleborus xylographus (Say)

BIOLOGY.—Unstudied. In species of this genus that are studied, haploid males are produced parthenogenetically. They are dwarfed and flightless. Diploid females are produced by mating between siblings or between a female parent and a male offspring. Infests *Quercus* spp., rare in other hardwoods. The galleries are made obliquely into sapwood in a horizontal plane to a depth of an inch or more, after which they branch, the arms following the annual rings (Beal and Massey 1945).

DISTRIBUTION AND NOTES.—CANADA: Ont., Que.; USA: twenty-two states (and D.C.) east of 100th meridian; Calif. (1 specimen), Tex. OREGON: 5 km NW Newberg, Yamhill Co., 20-VI-1970, black light trap, K. J. Goeden (1 ODAC).

Trypophloeus striatulus (Mannerheim)

BIOLOGY.—Monogynous. Infests outer bark of *Salix* spp., most commonly *S. scouleriana*; also recorded from *Alnus* spp. May reinfest stem progressively downward for several generations. Cave type egg gallery; larvae mine shallowly under bark.

DISTRIBUTION AND NOTES.—CANADA: Newf., N.S., Que., Yukon; USA: Alas., Colo., Ida., Minn., Ut. OREGON: Hot Springs Campground, Hart Mtn. Natl. Antelope Refuge, Lake Co., 14-VIII-1990, *Salix scouleriana*, M. M. Furniss and J. B. Johnson (34 WFBM, 5 ODAC). Infesting necrotic bark lesions in a live stem having a deep frost crack. Diameter of infested part: 5-10 cm. Mature larvae present.

Trypophloeus thatcheri Wood

BIOLOGY.—Monogynous. Infests outer bark of standing, unhealthy or dying *Populus tremuloides*. Cave type egg gallery; larval mines confined to outer bark.

DISTRIBUTION AND NOTES.—CANADA: B.C.; USA: Calif., Ida. OREGON: Hot Springs Campground, Hart Mtn. Natl. Antelope Refuge, Lake Co., 14-VIII-1990, *Populus tremuloides*, M. M. Furniss and J. B. Johnson (27 WFBM, 5 ODAC). Adults attacking and walking on bark of a dying, 15-cm-diameter tree.

Procryphalus mucronatus (LeConte)

BIOLOGY.—Monogynous. Infests *Populus tremuloides*. Prefers soft, fermenting, dead bark; usually follows primary invasion by *Trypophloeus populi* Hopkins (Petty 1977). The gallery is narrower and the bark overlying the gallery is thicker than that of *T. populi* Hopkins (and presumably *T. thatcheri*). One and one-half to two annual generations (Utah), overwintering as larvae and adults. Eggs appear first in late May.

DISTRIBUTION AND NOTES.—CANADA: Alta., B.C.; USA: Alas., Colo., Ida., Mont., Nev., N.M., Ut. OREGON: Hot Springs Campground, Hart Mtn. Natl. Antelope Refuge, Lake Co., 14-VIII-1990, *Populus tremuloides*, M. M. Furniss and J. B. Johnson (9 WFBM). Infesting stem of a 26-cm-diameter tree. Jackman Park, Steens Mtn., Harney Co., 14-VIII-1990, *Populus tremuloides*, M. M. Furniss and J. B. Johnson (14 WFBM, 10 ODAC). Attacking lower stem of a 25-cm-diameter dead tree (foliage shed, bark moist).

Pityophthorus scalptor Blackman

BIOLOGY.—Presumably polygynous. Infests small branches of living pines.

DISTRIBUTION AND NOTES.—CANADA: B.C.; USA: Calif., Ida. OREGON: 15 km N Palmer-Junction, Union Co., 16-VIII-1990, *Pinus ponderosa*, M. M. Furniss and J. B. Johnson (2 ♀, 2 ♂ WFBM). Infesting 1-cm-diameter freshly faded lower branch on a live, merchantable tree. Each gallery contained only one female and one male, no eggs or larvae; they appeared destined to overwinter before reproducing.

Monarthrum dentigerum (LeConte)

BIOLOGY.—Not studied. Infests *Quercus* spp. Most species of *Monarthrum* are polygynous and their galleries branch from a radially oriented entrance tunnel in the xylem. Larvae of this genus develop in niches, apparently feeding on a mixture of ambrosial fungus that grows on gallery walls and xylem of the host tree.

DISTRIBUTION AND NOTES.—MEXICO: Baja California; USA: Ariz., Calif., Tex. OREGON: Medford, Jackson Co., 18-VIII-1968, black light trap (1 ODAC).

OREGON SCOLYTIDAE

HYLESININAE

Hylastini

Scierus annectens LeConte
Hylurgops porosus (LeConte)
Hylurgops reticulatus Wood
Hylurgops rugipennis rugipennis (Mannerheim)
Hylurgops subcostulatus subcostulatus (Mannerheim)
Hylastes gracilis LeConte
Hylastes longicollis Swaine
Hylastes macer LeConte
Hylastes nigrinus (Mannerheim)
Hylastes ruber Swaine
Hylastes tenuis Eichhoff

Hylesinini

Hylastinus obscurus (Marsham)
Hylesinus californicus (Swaine)
Hylesinus oregonus (Blackman)
Alniphagus aspericollis (LeConte)
Alniphagus hirsutus Schedl

Tomicini
Xylechinus montanus Blackman
Pseudohylesinus dispar dispar Blackman
Pseudohylesinus dispar pullatus Blackman
Pseudohylesinus granulatus (LeConte)
Pseudohylesinus nebulosus nebulosus (LeConte)
Pseudohylesinus nobilis Swaine
Pseudohylesinus pini Wood
Pseudohylesinus sericeus (Mannerheim)
Pseudohylesinus sitchensis Swaine
Pseudohylesinus tsugae Swaine
Dendroctonus brevicomis LeConte
Dendroctonus jeffreyi Hopkins
Dendroctonus ponderosae Hopkins
Dendroctonus pseudotsugae Hopkins
Dendroctonus rufipennis (Kirby)
Dendroctonus valens LeConte

Phloeotribini
Phloeotribus lecontei Schedl

Phloeosinini
Phloeosinus antennatus Swaine
Phloeosinus cupressi Hopkins
Phloeosinus fulgens Swaine
Phloeosinus hoferi Blackman
Phloeosinus punctatus LeConte
Phloeosinus scopulorum scopulorum Swaine
Phloeosinus sequoiae Hopkins
Phloeosinus serratus (LeConte)
Phloeosinus vandykei Swaine

Hypoborini
Chaetophloeus heterodoxus (Casey)

Polygraphini
Carphoborus intermedius Wood
Carphoborus piceae Wood
Carphoborus pinicolens Wood
Carphoborus ponderosae Swaine
Carphoborus sansoni Swaine
Carphoborus vandykei Bruck
Polygraphus rufipennis (Kirby)

SCOLYTINAE

Scolytini
Scolytus laricis Blackman
Scolytus monticolae Swaine
Scolytus multistriatus (Marsham)
Scolytus opacus Blackman
Scolytus oregoni Blackman
Scolytus piceae (Swaine)
Scolytus praeceps LeConte
Scolytus rugulosus (Müller)
Scolytus subscaber LeConte
Scolytus tsugae (Swaine)
Scolytus unispinosus LeConte
Scolytus ventralis LeConte

Micracini
Hylocurus hirtellus (LeConte)

Crypturgini
Dolurgus pumilis (Mannerheim)
Crypturgus borealis Swaine

Dryocoetini
Dryocoetes affaber (Mannerheim)
Dryocoetes autographus (Ratzeburg)
Dryocoetes confusus Swaine
Dryocoetes sechelti Swaine

Ipini
Pityogenes carinulatus (LeConte)
Pityogenes fossifrons (LeConte)
Pityogenes knechteli Swaine
Pityokteines elegans Swaine
Pityokteines lasiocarpi (Swaine)
Pityokteines minutus (Swaine)
Pityokteines ornatus (Swaine)
Orthotomicus caelatus (Eichhoff)
Ips concinnus (Mannerheim)
Ips emarginatus (LeConte)
Ips integer (Eichhoff)
Ips latidens (LeConte)
Ips mexicanus (Hopkins)
Ips montanus (Eichhoff)
Ips paraconfusus Lanier
Ips pini (Say)
Ips plastographus maritimus Lanier
Ips plastographus plastographus (LeConte)
Ips tridens engelmanni Swaine
Ips tridens tridens (Mannerheim)

Xyloterini
Trypodendron betulae Swaine
Trypodendron lineatum (Olivier)
Trypodendron retusum (LeConte)
Trypodendron rufitarsis (Kirby)

Xyleborini
Xyleborus californicus Wood
Xyleborus dispar (Fabricius)
Xyleborus intrusus Blandford
Xyleborus xylographus (Say)
Xyleborinus saxeseni (Ratzeburg)

Cryphalini
Trypophloeus salicis Hopkins
Trypophloeus striatulus (Mannerheim)
Trypophloeus thatcheri Wood
Procryphalus mucronatus (LeConte)
Procryphalus utahensis Hopkins
Cryphalus pubescens Hopkins
Cryphalus ruficollis ruficollis Hopkins

Corthylini
Pseudopityophthorus pubipennis (LeConte)
Conophthorus ponderosae Hopkins
Pityophthorus boycei Swaine
Pityophthorus confertus Swaine
Pityophthorus confinis LeConte
Pityophthorus digestus (LeConte)
Pityophthorus electus Blackman
Pityophthorus jeffreyi Blackman
Pityophthorus murrayanae Blackman
Pityophthorus nitidulus (Mannerheim)
Pityophthorus nitidus Swaine
Pityophthorus pseudotsugae Swaine
Pityophthorus scalptor Blackman
Pityophthorus toralis Wood
Pityophthorus tuberculatus Eichhoff
Gnathotrichus retusus (LeConte)
Gnathotrichus sulcatus (LeConte)
Monarthrum dentigerum (LeConte)
Monarthrum scutellare (LeConte)

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RIFFLE BEETLES (COLEOPTERA: ELMIDAE) OF DEATH VALLEY NATIONAL MONUMENT, CALIFORNIA

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ABSTRACT—Three species of Elmidae occur in Death Valley National Monument: *Stenelmis calida* is in three springs in the Ash Meadows area; *Microcylloepus formicoideus* is only in Travertine Springs; and *Microcylloepus similis* is in several springs throughout Death Valley and Ash Meadows. Only permanent springs support elmids. Considerable morphological variation occurs in the disjunct populations of *M. similis*. The evolution of elmids in Death Valley National Monument is equivalent to that of the local pupfish (*Cyprinodon* spp.).

Key words: Death Valley, Insecta, Coleoptera, Elmidae, distributions, desertification, evolution.

Death Valley National Monument (DVNM) is located mostly in southeastern California, with two small extensions into southwestern Nevada. DVNM includes Death Valley proper, its adjacent mountain ranges, and the Ash Meadows area of Nevada which surrounds Devil's Hole. Biogeographically this is a transition area between the Mojave Desert and the Basin and Range Desert. Desert conditions here are the result of the drier and warmer post-Pleistocene climate and a rain-shadow effect from the Panamint Mountains, the Sierra Nevada, and the Coast Range mountains to the west.

Water sources in DVNM are unexpectedly common. Palmer (1980) cites over 100 springs alone. Hunt (1975) has classified these springs into four types based upon volume of discharge and geomorphic origin. The Amargosa River flows (when it does!) into the southern end of Death Valley. Two permanent streams, Salt Creek and Furnace Creek, are located in the central portion of DVNM. Numerous "wells" (shallow, subsurface water sources) and "seeps" are to be found scattered throughout DVNM. These are not reliable water sources, being more or less intermittent. Wherever a water source does occur, however, it may not be very amenable to aquatic organisms because of lethal temperatures and/or salinities. Discussions of the local hydrology can be found in Hunt et al. (1966) and Soltz and Naiman (1978).

Of the aquatic organisms occurring in DVNM, only the fishes have been studied extensively. Soltz and Naiman (1978) reviewed the past work and presented an excellent synthesis, particularly so for *Cyprinodon* spp. (pupfish). For aquatic insects, studies have been primarily descriptions of new species and their type localities [e.g., Chandler (1949), Usinger (1956)]; only one study (Colburn 1980) directly addressed the ecology of any species. However, Deacon (1967, 1968) discussed insects as part of the community ecology of Saratoga Spring.

During a vacation I found a single specimen of a riffle beetle in Saratoga Spring at the south end of DVNM. That chance discovery led me to embark on a survey of the water sources in DVNM to determine if other elmids (riffle beetles) occurred there, and, if so, in which sources.

METHODS

Water Sources

The water sources examined were chosen primarily because of their accessibility. Those that required more than a day's travel by auto and/or foot were not examined. In all, 27 water sources were examined in Death Valley and its environs, and in Ash Meadows. Death Valley water sources include: Grapevine Spring, Scotty's Castle Spring, Mesquite Spring, Daylight Spring, Hole-in-the-Wall Spring, Midway Well, Stovepipe Wells, Salt Creek, Nevare's

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Springs, Texas Spring, Travertine Springs, Emigrant Spring, Navel Spring, Tule Spring, Badwater, Shorty's Well, Eagle Borax Spring, Warm Spring, Ibex Spring, and Saratoga Spring. Ash Meadows water sources include: Indian Spring, School Spring, Devil's Hole, Point of Rocks Spring, Jackrabbit Spring, Big Spring, and an unnamed spring.

The only permanent water sources are large-volume springs on the east side of Death Valley and in Ash Meadows, and Devil's Hole. No water flows from Devil's Hole, but here the surface of the ground intersects the hydrologic head of the groundwater so water is always present in the bottom of a large crevice. These permanent sources are all connected with the Ash Meadows Groundwater Basin.

Collections

All of the above water sources were examined for the presence of riffle beetles. Where possible, collecting was accomplished with a standard kick-net. However, many of the seeps and wells had such low discharge and/or narrow width that collection could be done only by manual removal of rocks and sticks for visual examination. Voucher specimens for all species collected were deposited in the author's collection at California State University–Sacramento.

RESULTS

Of the 27 water sources examined, 8 were found to contain populations of elmids (Table 1). *Stenelmis calida* Chandler was still resident in Devil's Hole, its type locality. However, during this survey two additional populations were located in nearby Indian Spring and Point of Rocks Spring. La Rivers reports unsuccessfully searching springs near Devil's Hole in an attempt to locate additional populations (Chandler 1949). It is not known whether these additional populations were missed or if they are the result of colonization or transplantation. The spring run coming from Indian Spring is very narrow and deeply incised into the desert floor, making it extremely inconspicuous.

Microcylloepus formicoideus Shepard occurred only at Travertine Springs (Shepard 1990). Near the spring heads (a complex of several upwellings) and for many meters below, *M. formicoideus* was the only elmid to be found. Further downstream, though, it co-occurs with *M. similis* (Horn). In the lower third of the spring run *M. similis* completely replaces *M. formicoideus*. *Microcylloepus similis* also occurs in several other springs: Grapevine Spring, Nevare's Springs, Saratoga Spring, Indian Spring, Point of Rocks Spring, and Big Spring.

TABLE 1. The occurrence of riffle beetles (Coleoptera: Elmidae) in water sources of Death Valley National Monument.

Water source	Average temp. (C)	Elevation (m)	Species[a]
Death Valley			
1. Grapevine Spring	25–29	820	2
2. Nevare's Springs	–	300	2
3. Travertine Springs	32–36	122	2,3
4. Saratoga Spring	26–29	46	2
Ash Meadows			
5. Indian Spring	24–30	705	1,2
6. Devil's Hole	"	735	1
7. Point of Rocks Spring	"	705	1,2
8. Big Spring	"	681	2

[a] 1 = *Stenelmis calida*, 2 = *Microcylloepus similis*, 3 = *Microcylloepus formicoideus*

All water sources inhabited by elmids were located either on the east side of Death Valley or in Ash Meadows. With the exception of Devil's Hole, these springs all exhibit permanent flow of a relatively large volume. Most of the water sources not inhabited by elmids are low-volume seeps (e.g., Daylight Spring), subsurface sources (e.g., Shorty's Well), or pooled water (e.g., Badwater).

(Note added after author review: Richard Zack [Washington State University] has found *S. calida* in Skruggs Spring and Mexican Spring in Ash Meadows [WDS].)

DISCUSSION

The major factor linking those springs inhabited by elmids is their association with the Ash Meadows Groundwater Basin. This large watershed undoubtedly maintains the constant flow required by elmids. The only large-volume spring not inhabited by elmids, Jackrabbit Spring, was pumped dry during a local battle over water rights.

Although it may at first seem incongruous to find riffle beetles in a desert area, one must remember that the regional desertification is a rather recent event, geologically and ecologically speaking. During the several Pleistocene glacial periods, and perhaps even before, the Basin and Range Desert was far cooler and wetter. The Death Valley area is thought then to have had a climate much like the present-day Lake Mono area, 240 km (150 mi) to the north (Hildreth 1976). Evidence from the distributions of fishes in the desert of California and Nevada and along the East Front of the Sierra Nevada suggests that many of the Pleistocene lakes overflowed their basins and were connected by extensive river systems (Miller 1946, Hubbs and Miller 1948, Soltz and Naiman 1978). Thus, pre-Pleistocene distributions of aquatic organisms would have been subject to changes during the Pleistocene. Ultimately, these distributions were then subjected to the influences of the warmer and drier, current interglacial period. Present distributions are, therefore, the sum of pre-Pleistocene distributions, Pleistocene dispersals, and post-Pleistocene vicariant strandings.

Small, isolated populations that were stranded in reliable water sources presented ideal situations for rapid evolution, given the small gene pools and lack of gene flow from other populations. These factors have been responsible for the quick proliferation of pupfish taxa in the Death Valley area (Soltz and Naiman 1978). This may also account for the speciation of *M. formicoideus*, the development of subspecies in *S. calida*, and the interpopulational variation in *M. similis*.

Stenelmis calida had been previously reported from Ash Meadows in the form of its nominate subspecies. A second subspecies, *S. c. moapa* La Rivers, occurs southeast of DVNM along the Muddy River in southern Nevada. Each of the various populations of *M. similis* exhibits minor morphologic variations, some even in the aedeagus. I have vacillated for a long time concerning the taxonomic status of these disjunct populations. However, since the genus needs revision, and because I suspect that the variation is ecologically induced, I have chosen to be conservative and not assign separate taxonomic status to any of the populations. Perhaps some enterprising future student will examine how constant warm temperatures influence morphologic expression in riffle beetles. If so, the springs of DVNM and the Basin and Range Desert would offer an excellent natural experiment, and the numerous populations of *M. similis* in those springs and spring runs would be choice study material.

The elmids of DVNM represent an invertebrate analog of the already well-documented evolution of pupfish of DVNM (see Soltz and Naiman 1978). *Microcylloepus formicoideus* is similar to *Cyprinodon diabolis* in being located in only one water source and in being very distinct from and smaller than its congeners. *Stenelmis calida* is similar to *C. salinus* and *C. milleri* in that there are two taxa (subspecies) that inhabit two separate locations along a once free-flowing water course (La Rivers 1949). *Microcylloepus similis* is similar to *C. nevadensis* in being widely distributed but having isolated, somewhat morphologically distinct populations throughout DVNM and surrounding areas.

Elmids, like most aquatic insects, accomplish dispersal primarily by flying adults. As the post-Pleistocene desertification proceeded, water sources in the DVNM area became smaller, fewer, and farther apart. A point eventually had to be reached at which aerial dispersal became hazardous. Mutations reducing the ability to fly would then be favored; indeed, relatively rapid fixation of these mutations in the population would be expected. It is not surprising, then, that adults of all three elmids occurring in DVNM are either apterous (wingless) or brachypterous (with incompletely developed wings), and subsequently incapable of flying.

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SIPHONAPTERA (FLEAS) COLLECTED FROM SMALL MAMMALS IN MONTANE SOUTHERN UTAH

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Key words: fleas, Siphonaptera, Utah, mammals.

Recent collections from various small mammals of southern Utah have helped to elucidate the distribution of fleas (Siphonaptera) within the state. Of special interest were fleas of mammals found in forested, high-mountain areas of the southernmost part of Utah—an area of complex topography containing habitat varying from low desert to subalpine coniferous forests. In particular, we sampled the small mammal flea fauna of the Abajo Mountains (San Juan County), the La Sal Mountains (Grand/San Juan counties), and the Pine Valley Mountains (Washington County). These ranges have been sparsely surveyed in this respect, as evidenced by review of the seminal work of Stark (1959). After excluding 22 records (13 ♂♂, 37 ♀♀) of the ubiquitous deer mouse flea *Aetheca wagneri* (Baker), which occurs in all counties of Utah (Beck 1955), we present and discuss the significance of 42 new records of 12 species of fleas. A parallel survey of fleas found in mammal nests will be presented elsewhere (Haas and Kucera, in preparation).

Mammal nomenclature is that of Hall (1981). However, designations of long-tailed vole subspecies should be considered tentative because of the present confused state of their taxonomy. Mammals were collected with Sherman live-traps at all localities except Pines campground, Pine Valley Mountains, and snap-traps were used at all three localities in the Pine Valley Mountains and at Oowah Lake campground, La Sal Mountains. An asterisk (*) denotes that the host specimen (or at least one host specimen) was deposited in the mammal collection of the University of Utah Museum of Natural History. Flea specimens are retained by the authors.

Hystrichopsylla dippiei truncata Holland, 1957

Peromyscus maniculatus rufinus. San Juan Co.: Abajo Mts., Dalton Springs campground, 2560 m, 8 September 1991; 1♂. *Microtus longicaudus alticola**. idem, 1♀.

Hystrichopsylla occidentalis sylvaticus Campos & Stark, 1979

*Peromyscus boylii utahensis**. Washington Co.: Pine Valley Mts., North Juniper Park campground, 2122 m, 10 November 1991; 3 ♀♀. *Peromyscus maniculatus sonoriensis*. Washington Co.: Pine Valley Mts., Pines campground, 2079 m, 12 June 1991; 1 ♀.

Fleas of the genus *Hystrichopsylla* are found on a variety of small mammals in mesic to moist habitats. These are the first records of *H. dippiei truncata* from southeastern Utah. Campos and Stark (1979) record *H. o. sylvaticus* from San Juan Co., but our records of this taxon are the first from southwestern Utah.

Corrodopsylla curvata curvata (Rothschild, 1915)

Sorex palustris navigator (Baird)*. Grand Co.: LaSal Mts., meadow at Oowah Lake, 2769 m, 15 June 1991; 1♂, 1♀ from each of two shrews.

The only previous published records from Utah of *C. c. curvata* are both from northern Utah: Rich Co. (Bear Lake; collection by Stanford published by Tipton and Allred [1951: 107]) and Salt Lake Co. (Wasatch Mts.; Egoscue 1988). These records are from unidentified

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Sorex spp. Records of *C. c. obtusata* ex water shrews are given from Tooele Co. by Egoscue (1966, 1988). Published records of *C. c. curvata* from southwestern states are sparse: Haas et al. (1973) record it from New Mexico. Additional collecting may reveal its presence in the Abajo Mts., since water shrews are known to occur there (Schafer 1991).

Rhadinopsylla sectilis sectilis (Jordan & Rothschild, 1923)

Peromyscus maniculatus sonoriensis. Washington Co.: Pine Valley Mts., North Juniper Park campground, 2119 m, 10 November 1991; 1♂.

This species is known from only one area of southern Utah (Garfield Co., vic. Panguitch, Stark 1959), but not previously from southwestern Utah. This specimen possesses 5 spines in the genal comb, as do other Utah specimens (Stark 1959, and unpublished data), but characters of the genitalia are clearly referable to *R. s. sectilis* rather than *R. s. goodi* (Hubbard 1941). Stark (1959) noted that the genal spine number of Utah specimens is not consistent with the original description of *R. s. sectilis*.

Catallagia decipiens Rothschild, 1915

Peromyscus maniculatus rufinus. San Juan Co.: Abajo Mts., Dalton Springs campground, 2560 m, 8 September 1991; 1 ♂. *P. m. rufinus*. idem, 1 ♂. *Tamias* sp. idem, 2 ♂♂. *P. m. rufinus*. Grand Co.: LaSal Mts., Oowah Lake campground, 2682 m, 15 June 1991; 1 ♂, 2 ♀♀.

These are apparently the first specific records published for that part of Utah south of the Colorado River. Beck (1955: Table 3) lists it as occurring in San Juan County.

Peromyscopsylla selenis (Rothschild, 1906)

Peromyscus maniculatus rufinus. San Juan Co.: Abajo Mts., Dalton Springs campground, 2560 m, 8 September 1991; 1 ♂. *Microtus longicaudus alticola**. idem, 1 ♂. *M. l. alticola*. idem, 1 ♀. *M. l. latus*. Washington Co.: Pine Valley Mts., Pines campground, 2079 m, 12 June 1991; 2 ♂♂, 1 ♀.

This species was not previously known from Utah south of the Colorado River. Johnson and Traub (1954) give a record from Iron County, bordering Washington County to the north. This species is most commonly collected from *Microtus* spp., but also from other small mammals sympatric with the voles.

Peromyscopsylla hesperomys adelpha (Rothschild, 1915)

Peromyscus maniculatus rufinus. Grand Co.: LaSal Mts., Oowah Lake campground, 2682 m, 15 June 1991; 1 ♂, 2 ♀♀.

Johnson and Traub (1954) record this species from Beaver, Box Elder, Millard, San Juan, and Washington counties.

Opisodasys keeni (Baker, 1896)

Peromyscus maniculatus sonoriensis. Washington Co.: Pine Valley Mts., N Juniper Park campground, 2119 m, 10 November 1991; 1 ♀ from each of three hosts. *Peromyscus boylii rowleyi*. idem (2122 m.), 3 ♀♀. *P. m. sonoriensis*. Washington Co.: Pine Valley Mts., Pines campground, 2079 m, 11 June 1991; 1 ♀. *P. m. sonoriensis*. idem, 12 June 1991, 1 ♀. *P. m. sonoriensis*. idem, 1 ♂. *Peromyscus crinitus* ssp. Washington Co.: below dam at Baker Dam Reservoir, foothills of Pine Valley Mts., 1463 m, 12 May 1991; 1 ♀.

No known records of this species from southern Utah are published other than that of Hubbard (1947:111, Garfield Co.). Stark (1959) noted that this species is collected only in mountainous areas or moist habitats. We have also found this to be true (unpublished data). *Peromyscus* spp. are the usual host.

Malaraeus telchinus (Rothschild, 1905)

Peromyscus maniculatus sonoriensis. Washington Co.: Pine Valley Mts., N Juniper Park campground, 2119 m, 10 November 1991; 2 ♂♂, 1 ♀. *P. m. sonoriensis*. idem, 1 ♂, 1 ♀. *P. m. sonoriensis*. idem, 2 ♀♀. *P. m. sonoriensis*. idem, 1 ♀. *Peromyscus boylii rowleyi*. idem, 1 ♀.

Malaraeus sinomus (Jordan, 1925)

Peromyscus crinitus ssp. Washington Co.: below Baker Dam Reservoir, foothills of Pine Valley Mts., 1463 m, 11 May 1991, 1 ♂, 4 ♀♀. *P. crinitus* ssp. idem, 12 May 1991, 1 ♂, 2 ♀♀. *P. crinitus* ssp. idem, 1 ♂, 4 ♀♀. *Peromyscus truei truei*. idem, 3 ♀♀. *P. t. truei*. idem, 1 ♂, 2 ♀♀. *P. boylii rowleyi*. idem, 1 ♂. *P. boylii rowleyi*. idem, 2 ♀♀.

Beck (1955: Table 3) lists *Malaraeus telchinus* as occurring in Washington County. Hubbard (1947: 200) gives the only specific record from southern Utah (Garfield Co.). However, several records of *M. sinomus* from desert areas of southern Utah are given by Stark

(1959). Also, many specimens of *M. sinomus* from *Peromyscus crinitus* were taken by the senior author in Snow Canyon (Washington Co.) incidental to the search for *Traubella grundmanni* Egoscue, 1989. *M. telchinus* seems to be like *O. keeni* in being found only in nondesert habitat.

Megabothris abantis (Rothschild, 1905)

Microtus longicaudus alticola. Grand Co.: LaSal Mts., meadow at Oowah Lake, 2676 m, 14 June 1991; 1♂, 1♀. *Peromyscus maniculatus rufinus*. idem, 1♀. *M. l. alticola*. idem, 1♀. *M. l. alticola*. idem, 15 June 1991, 1♂, 1♀. *M. l. alticola*. San Juan Co., Abajo Mts., Dalton Springs campground, 2560 m, 8 September 1991, 1♂.

Beck (1955: Table 3) listed this species as occurring in Beaver, Iron, Sevier, and Wayne counties. This was apparently overlooked by Stark (1959: 196), who stated, "This flea appears confined to the northern half of the state." Egoscue (1988) reported collecting one male specimen from a pika at Johnson Reservoir, Sevier County, in south central Utah. The distribution map of Haddow et al. (1983: Map 76) indicates a locality record in that same region of Utah. Our records are the first for southeastern Utah. *Megabothris abantis* is usually found on various species of *Microtus*.

Eumolpianus eumolpi americanus (Hubbard, 1950)

Tamias sp. San Juan Co.: Abajo Mts., Dalton Springs campground, 2560 m, 8 September 1991; 2♀♀.

These specimens seem closer to *E. e. americanus* than to *E. e. eumolpi* recorded by Beck (1955, then in the genus *Monopsyllus*). Several of the type specimens were collected in San Juan County (Hubbard 1950). Johnson (1961) indicates that intergradation between *E. e. americanus* and *E. e. eumolpi* occurs in the county.

In summary, the significant findings among 64 collection records of 13 species of fleas are as follows: the first records south of the Colorado River in southeastern Utah for *Hystrichopsylla dippiei truncata*, *Corrodopsylla c. curvata*, *Peromyscopsylla selenis*, and *Megabothris abantis*; and the first in Washington County, southwestern Utah, for *H. occidentalis sylvaticus*, *Rhadinopsylla s. sectilis*, *P. selenis*, and *Opisodasys keeni*.

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NOTES ON SPIDER (THERIDIIDAE, SALTICIDAE) PREDATION OF THE HARVESTER ANT, *POGONOMYRMEX SALINUS* OLSEN (HYMENOPTERA: FORMICIDAE: MYRMICINAE), AND A POSSIBLE PARASITOID FLY (CHLOROPIDAE)

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Key words: Pogonomyrmex salinus, *harvester ants*, Euryopis formosa, Xysticus, *spider predators*, Incertella, *parasite*.

Spiders are known predators of ants. Pressure exerted by consistent spider predation can alter the behavior of ant colonies (MacKay 1982) and may be a selective pressure contributing to the seed-harvesting behavior of *Pogonomyrmex* (MacKay and MacKay 1984). We observed the spider *Euryopis formosa* Banks (Araneae: Theridiidae) capture and transport workers of the harvester ant (*Pogonomyrmex salinus* Olsen [Hymenoptera: Formicidae, Myrmicinae]) in southeastern Idaho. Additional observations revealed a crab spider of the genus *Xysticus* preying on *P. salinus* and the presence of a chloropid fly (*Incertella*) that may have been parasitizing the moribund prey subdued by the spider.

STUDY SITE

One collection site is located along Road T-20 (Butte County, T4N, R31E, S6) on the Idaho National Environmental Research Park (INERP) in the cold desert of southeastern Idaho. The second set of observations was made on the INERP (Clark County, T7N, R31E, S34, along Highway 28). Voucher specimens of all species have been deposited at the Orma J. Smith Museum of Natural History, Albertson College of Idaho, Caldwell, Idaho 83605 USA (CIDA).

RESULTS AND DISCUSSION

On 3 July 1988, 1020 h, at the Butte County collection site we collected a single individual of *Euryopis formosa* Banks (Araneae: Theridiidae) that was carrying a worker of *Pogonomyrmex salinus* Olsen (Hymenoptera: Formicidae, Myrmicinae) across a large area of basalt rock. The ants were actively foraging in the area. The air temperature (shaded) was 31 C and the soil surface (in the sun) was 39.5 C. No other spiders of this species were encountered. Prey capture was not observed.

On 31 August 1991 at 1725 h at the Clark County site we observed a crab spider of the genus *Xysticus* preying on *P. salinus* about 20 cm from the ant nest entrance. The ants were still actively foraging at this time. One spider was riding on the ant in the shelter of an isolated clump of Indian ricegrass (*Oryzopsis hymenoides*) at the edge of the ant mound. The ant was initially very active, walking around an old grass stem, while the spider made periodic attacks on the ant. As time progressed, involuntary spasms in the ant increased. The spider was generally oriented toward the posterior of the ant, biting it at the base of the petiole. Sometimes the spider was perpendicular to the ant, holding on to the ant with only its mandibles. After five minutes the ant fell onto its side and movements slowed. At 1740 h only its antennae were moving slightly, and a minute later the spider moved the ant under a small stick. Two small flies approached the ant and one flew onto its head. Occasional movements (jerks) of the ant's legs were observed at 1751 h. At this time we collected the spider, the ant, and one of the flies (WHC #9170). The fly is a female *Incertella* (Diptera: Chloropidae) and may represent an undescribed species. Brown and Feener (1991) have found the phorid *Apocephalus paraponerae* selectively parasitizing moribund workers of *Paraponera clavata*. It may be that these *Incertella* flies are seeking a similar host and opportunistically exploiting the spider prey. The flies were not observed to interact with living, active ants.

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At 1740 h we noticed a second spider, *E. formosa*, on the same ant mound. This spider oriented uphill on the side of the mound, facing the ant nest entrance. At 1742 h an ant walked over and slightly past the spider, apparently failing to recognize the predator's presence. The spider remained motionless as the ant passed, then spun around and mounted the ant's gaster. The spider released the ant and moved to face it. The ant began convulsing at this time, while the spider sat 1 cm away from the ant (facing away from the ant). By 1745 h no motion was observed in the ant and at 1746 h the spider climbed onto the ant. The ant was on its side with the spider on top facing the gaster. A fly similar to those mentioned above moved onto the head of the ant. At 1747 h the spider was dragging the ant across the mound using a web sling, as previously described by Porter and Eastmond (1982) for the spider *E. coki* in southeastern Idaho. The spider dragged the ant to the edge of the mound and into the grass clump mentioned earlier. Several other worker ants were observed strung up in the grass clumps. At this point we collected the spider (WHC #9171).

The spider genus *Euryopis* is known to prey on ants (Levi 1954, Carico 1978), including harvester ants of the genus *Pogonomyrmex* in North America (MacKay 1982, Porter and Eastmond 1982). MacKay (1982) has reported *E. californica* preying on *P. rugosus* in southern California.

Prey of *E. formosa* has not previously been reported (Levi 1954), nor has the spider been reported from the INERP (Levi 1954, Allred 1969). Levi (1954) gives the distribution of the species over most of Idaho except for the southwestern corner, so its presence here was expected. Allred (1969) reported a related species, *Euryopis scriptipes* Banks, from the southeastern border of INERP during July. *Pogonomyrmex salinus* is the dominant seed-harvesting ant on the INERP, occurring in almost all of its plant communities (Blom et al. 1991).

Porter and Eastmond (1982) found *Euryopsis coki* Levi to be a common predator of *Pogonomyrmex owyheei* (=*P. salinus*) in southeastern Idaho during July and August. These small gray spiders capture ants on their mounds and drag them away by a web sling attached to the ant and to the tip of the spider's abdomen. *Euryopsis formosa* is found from central California north to British Columbia and east to Wyoming (Levi 1954). *E. formosa* may also be an important predator of *P. salinus* at this site and of *Pogonomyrmex* species in the western United States. The relatively greater precision and speed with which *Euryopsis* subdued and transported the *P. salinus* prey suggests an established predator-prey relationship.

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